PLANT-BREEDING

COMMENTS ON THE EXPERIMENTS
OF NILSSON AND BURBANK

BY

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CHICAGO
THE OPEN COURT PUBLISHING CO.
LONDON: KEGAN PAUL, TRENCH, TRÜBNER & CO., LTD.
1907

PREFACE

Under the influence of the work of Nilsson, Burbank, and others, the principle of selection has, of late, changed its meaning in practice in the same sense in which it is changing its significance in science by the adoption of the theory of an origin of species by means of sudden mutations. The method of slow improvement of agricultural varieties by repeated selection is losing its reliability and is being supplanted by the discovery of the high practical value of the elementary species, which may be isolated by a single choice. The appreciation of this principle will, no doubt, soon change the whole aspect of agricultural plant breeding.

Hybridization is the scientific and arbitrary combination of definite characters. It does not produce new unit-characters; it is only the combination of such that are new. From this point of view the results of Burbank and others wholly agree with the theory of mutation, which is founded on the principle of the unit-characters.

This far-reaching agreement between science and practice is to become a basis for the further development of practical breeding as well as of the doctrine of evolution. To give proof of this assertion is the main aim of these Essays.

Some of them have been made use of in the delivering of lectures at the universities of California and of Chicago during the summer of 1906 and of addresses before various audiences during my visit to the United States on that occasion. In one of them (II. D.), the main contents have

been incorporated of a paper read before the American Philosophical Society at their meeting in honor of the bi-centennary of the birth of their founder, Benjamin Franklin, April, 1906.

The results of Nilsson have been published only in the Swedish language; those of Burbank have not been described by himself. My arguments for the theory of mutation have been embodied in a German book, "Die Mutationstheorie" (2 vols. Leipsic, Veit & Co.), and in lectures given at the University of California in the summer of 1904, published under the title of "Species and Varieties; their Origin by Mutation." A short review of them will be found in the first chapter of these Essays.

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I

EVOLUTION AND MUTATION

In the beginning of the last century Lamarck founded the theory of a common descent for all living beings. It afforded him the only possible means of explaining systematic affinity. He assumed that the influence of the environment was capable of changing the characters of the organisms, and of fitting them for their life conditions. His evidence, however, was very scanty and therefore he failed in convincing his contemporaries.

Half a century afterward Darwin brought together such an overwhelming mass of evidence that opposition had to give in. His main point was one of comparative investigation. At his time it was universally assumed that species had been created as such, but that subspecies and varieties had been derived from them according to natural laws. Darwin proved that no such distinction between species and subspecies exists. Their marks are of the same nature, and if a natural origin is assumed for one group, it must be conceded for the other too. The same holds good for genera and families, and even for the higher divisions of the system.

Moreover, Darwin showed that the sequence of the appearance of organisms during geological times finds a natural explanation on the assumption of the theory of descent, and that the geographical distribution of animals and plants is exactly as we should expect it to be if their common origin were the main factor in assigning them their special domains.

These broad proofs of the theory of evolution are quite independent of the question by which means and in what way new species are produced from the existing ones. This question, however, appeals more directly to the imagination,

and Darwin collected all the evidence concerning it which he could find. The rapid victory gained by his views has been due mainly to his discussion of this minor point.

Direct observations concerning the first appearance of species in nature were not at hand. In agriculture and in horticulture, however, numerous observations had been made, and for a number of races and varieties the origin was historically known. Distinct methods were in use to guide these changes and to produce varieties which would comply with the demands of practice. The grand principle of all these methods was selection. Selection means guiding the changes in the specific characters of organisms by cutting off all those which are changing in undesirable ways, and reserving for reproduction only those which differ advantageously from the average.

Darwin proved that the origin of species in nature must be the same phenomenon as the origin of races and varieties in culture. He showed that in nature an analogous process of selection is steadily active. More seeds are produced and more children are born than can possibly survive, and the decision as to which are to live and which must die depends, on one side, on the life conditions and, on the other, on the distinctive qualities of the competing individuals. Of course, in the single instances survival depends mainly on chance, but in the long run the different chances may be assumed to annul one another's influence, and the decision falls to individual excellences and life conditions. In this way the latter can be said to make a choice of the individuals best fitted for the local conditions and this is what is now universally known as *the principle of natural selection.* It guides evolution, keeping it in the useful ways, and destroys all that try to diverge in opposite directions.

The theory of common descent is Darwin's theory, since it has been founded by him on so broad a basis of facts as to

insure almost universal acceptance. The theory of natural selection is one of the means by which this position has been reached. It is the application of the breeding practice to the phenomena of nature at large. Darwin's theory is often designated as the theory of natural selection. This is however, not the same as the theory of descent. The idea of descent with modification, which now is the basis of all evolutionary science, is quite independent of the question as to how, in the single instances, the change of one species into another has actually taken place. The theory of descent remains unshaken even if our conception concerning the mode of descent should prove to be in need of revision.

Such a revision has become necessary by the gradual development of the study of variability. Darwin has demonstrated that all the individuals of a given species differ from one another to some extent, and that many of these differences increase or lessen their chances of survival. A struggle for life ensues, and, sooner or later, the unfit individuals succumb, thereby leaving the average of the species changed to some slight degree. Differences between isolated local races afford the means of studying the efficiency of this process of variability and selection. The question arises, however, as to how far this variability may go under the influence of this guidance. Is it limited or unlimited? Can it proceed during centuries and in the same direction, augmenting the differences to any extent, or is it bound by its original average condition, without being able to diverge far from it? Can it produce new characters and new qualities or is it limited to changes of degree in those that already exist? To all these, and many other questions, an answer could not be given at the time of Darwin, the evidence being too incomplete. It was necessary, however, to make a decision of some kind and thus it was universally assumed that the changes by which species originate are slow, almost invisible,

and may accumulate, in the lapse of time, to any degree. All of the characters of living organisms were simply assumed to be due to this slow process of gradual evolution guided by natural selection.

Here, however, a first difficulty arose. We do not observe actual specific changes in nature. To meet this objection Darwin assumed the changes to be so slow as to be invisible to us. Even the life time of a man would not be sufficient to control them. By this supposition the evolution of a flower or a seed or of highly differentiated organs (such as the leaves of insectivorous plants) would require an enormous time. From this a calculation could be made as to the time required for the whole range of evolution of the vegetable and animal kingdoms. The result was that many thousands of millions of years were considered to be the smallest amount that would account for the development of life on earth from the very first beginning until the appearance of mankind.

Physicists and astronomers have objected to this conclusion. The objection has been brought forward from the time when Darwin published his calculation. It has never relented and has often threatened to impair the whole theory of descent. The results of physical and astronomical calculations concerning the age of life on this earth differ so widely from the demands made by the theory of slow evolution as to be considered incompatible with them. The deductions made by Lord Kelvin and others, from the central heat of the earth, from the rate of the production of the calcareous deposits, from the increase of the amount of salt in the water of the seas, and from various other sources, indicate an age for the inhabitable surface of the earth of between twenty and forty millions of years only. This large discrepancy has always been a weapon in the hands of the opponents of the evolutionary idea, and there can be no

doubt that it proves that the current view of extremely slow and almost invisible changes must be abandoned.

Shortly after the publication of Darwin's Origin of Species, the Belgian anthropologist, Quetelet, submitted the variability in measurement of the different parts of the human body to a statistical investigation. He discovered that this kind of variability follows distinct laws and that these laws agree, in the main, with the law of probability. Small divergences from the average are numerous, larger discrepancies are rare, and the rarer, the larger they are. Variability is thereby limited, and is subject to a return to the average condition. It may be moved from this average, to some extent, by a change in the outward conditions or by a repeated selection in one direction; but, as soon as these causes and this selection cease to work, a return to the average is unavoidable. Variability may augment or diminish the qualities; it is linear, consisting of changes along a simple line, some being positive and others being negative, but it does not strike into new directions. It is no source of new qualities. The phenomena which are controlled by this law and which are bound to such narrow limits cannot be a basis for the explanation of the origin of species. It governs quantities and degrees of qualities, but not the qualities themselves. Species, however, are not, in the main, distinguished from their allies by quantities or by degrees — their very qualities may differ.

From this discussion it may be seen that the slow and gradual changes of ordinary variability and the production of new characters are not of the same order. Variability, in the ordinary sense of the word, is a broad conception. It must be subdivided for the purpose of scientific investigation. The phenomena that follow Quetelet's law are now considered as one group, which is called fluctuating variability or fluctuation, since the individual qualities fluctuate around

their average. The processes by which new qualities are produced must be studied separately. Under the assumption that these processes are neither slow nor invisible, but consist in leaps and jumps such as are popularly indicated by the name of sports, they are now called mutations, and this great subdivision of the phenomena of variability is designated, in consequence thereof, as mutability.

Darwin was well aware of the existence of different cases of variability, and of the possibility of their bearing on the theory of evolution. He considered the assumption of an origin of species in nature by leaps and sports, such as were observed to occur among horticultural plants. He pointed out that the affinity of closely allied species can be explained on this assumption as well as by slow changes. If we consider all the varieties and subspecies of apples, or beets, or of one of the cereals, and assume thousands of years for their production, the changes may have been brought about by rare sports as well as by long continued changes; the effect, at the present time, would be the same. Darwin agreed that this possibility could not be denied and that it was a very weak point in his hypothesis of slow evolution.

The mutations must not be assumed to be considerable changes. From a study of the differences among small species, we may form some conclusion as to their probable size. Common observation shows the difference between allied species, ordinarily, to be quite striking; but a little discussion and a closer inspection will easily prove that, in such cases, the differences are due to more than one, and often to numerous, characters. In groups (such as brambles, roses, buttercups, willows, and many others), where large numbers of species are closely allied, the differences between any two of them become smaller, and, the number of distinct forms increasing, the distinction, in the end, may become reduced to one single differential mark for each two

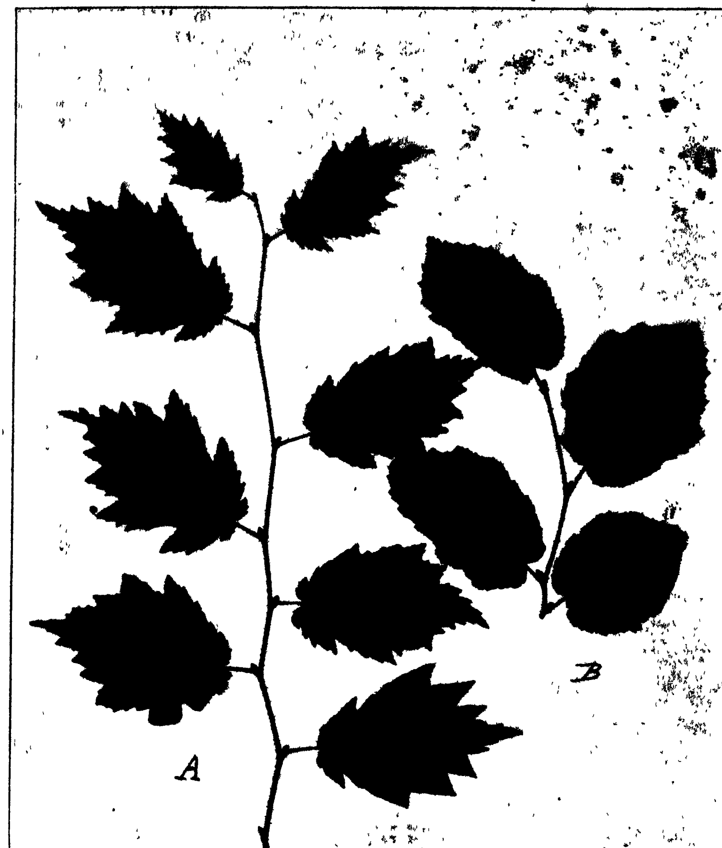


Fig. 1 A. The Oak-leaved Hazelnut (*Corylus Avellana laciniata*), a natural sport of the ordinary hazelnut (B).

neighboring types. Such differences must be assumed to be produced each by a single mutation. By this means the significance of the mutations may best be judged, and whenever species differ from their nearest allies in a higher degree, the inference is allowed that they have been originated by more than one mutation.

Since the publication of Darwin's theory, the probability of such sudden changes playing an important part in the evolution of species has always found some support. Of late, the evidence has increased in this direction, especially under the influence of Cope. Discontinuous evolution has been defended among palæontologists by Dollo, among zoölogists by Bateson, and among botanists by Korshinsky. This Russian author compiled the history of a large number of varieties from the widely scattered horticultural literature and showed that, in almost all cases where the history of the origin of a variety was recorded, it originated suddenly. Many other varieties, especially among trees and shrubs, have been discovered as such in the field, and, although their origin is not historically known, the constant absence of intermediates pleads vigorously for the explanation of their differential qualities by mutation.

The conception of mutations agrees with the old view of the constancy of species. This theory assumes that a species has its birth, its lifetime, and its death, even as an individual, and that throughout its life it remains one and the same. Thus it is only natural that wild species are almost always observed to be constant, since by a mutation they do not change themselves but simply produce a new type. This is allied to its ancestor as a branch is to a tree, the stem continuing its own growth, no matter how many branches it produces. Just so a species may produce quite a number of new forms without being changed itself, in the the least, thereby. Among palæontologists Scott has given

forth this same view. According to his conception, species are derived from one another by small shocks. Each shock caused the old limits to be transgressed; but, after it, the new species remained unchanged until, perhaps after centuries, a new shock made it transgress its new limits. Each single type (be it species, subspecies, or variety) is thus wholly constant from its first appearance and until the time it disappears, either after, or without, the production of daughter species.

On the ground of the mutation theory, there is a struggle for life among species as well as among individuals. There is selection, also, between competing species and among the individuals of the same species; the fittest will survive,— but this holds good for species as well as for individuals. As to individuals, natural selection may, to some extent, cause a divergence from the average type. But among species, natural selection is the most potent factor, since it eliminates some and thereby protects and favors others. Thus we come to the conclusion that natural selection is as active as Darwin assumed it to be, and is as pre-eminent a factor in the process of evolution. It causes the survival of the fittest; but it is not the survival of the fittest individuals, but that of the fittest species, by which it guides the development of the animal and vegetable kingdoms.

Summing up the main points of this discussion, we may sketch the origin of species, according to the theory of mutation, in the following manner. Species are derived from other species by means of sudden small changes which, in some instances, may be scarcely perceptible to the inexperienced eye. From their first appearance they are uniform and constant, when propagated by seed; they are not connected with the parent species by intermediates and have no period of slow development before they reach the full display of their characters. They do not always arise, but

only from time to time. A parent species may produce its offspring separately at intervals, or in larger numbers during distinct mutating periods. After this production, the old species is still the same as it was before, and it subsists in the midst of its children. New forms are produced by the old, either in one, or a few, or in numerous individuals; in the latter case, the chance of survival is evidently enhanced. Some young species will be better fitted for their life-conditions than others, and the struggle for life will induce a selection among them by which the fittest survive. Even as the new species are produced locally and as the effect of local causes, the struggle for life and natural selection decide concerning the survival according to the local conditions. These conditions thus have a twofold significance for the development of the pedigree of the main groups of plants and animals, but it is probable that they determine the lines of progress chiefly by their selective activity.

The main arguments in the discussion of the production of species by slow changes or by mutations were taken by Darwin from the experience of agricultural and horticultural breeders. Therefore it is desirable to inquire into their real significance. Do they support the one or the the other view? Darwin assumed that they gave proof of slow changes, and took his arguments mainly from the agricultural side. In horticulture, however, as we have seen in discussing Korshinsky's work, the probability is on the other side. In my experiments on mutability I have shown that it is possible to repeat and control the origin of horticultural and analogous varieties under strict experimental precautions, and that the full proof may be given that they originate at once, and not by a slow process of changes. They may, in the first instance, appear with the full display of their average character, or only with a small indication of it as an extreme variant of its fluctuation, but in the latter

case the average is often reached after one more generation.

I observed the origin of the peloric toadflax and of a double marigold, and produced, almost artificially, the twisted variety of a Dracocephalum.

In the case of the toadflax, Linaria vulgaris peloria, the change came suddenly, and more or less unsuspectedly, after a culture of about eight years. The ordinary form produces, from time to time, some few five-spurred, regular or peloric flowers. At once an individual arose which had such flowers only. The next year the mutation was repeated. The seeds of the mutated individuals reproduced the new variety almost exclusively, and each plant of it had peloric flowers only. No intermediates were observed, neither in the number of the spurs of the flower nor in the number of the peloric flowers on the plants. It was as sudden a change as any horticultural sport, but its ancestry had been purely fertilized and carefully recorded so as to leave no doubt concerning the real nature of the mutation.

The double variety of the corn-marigold (Chrysanthemum segetum) arose in my garden in a culture in which I was increasing the number of the ray-florets by continuous selection. During four years I had succeeded in increasing this number to about sixty on each head, starting from the cultivated variety, with an average of twenty-one. All the ray-florets, however, belonged to the outer rows of the heads, as in the original variety. At once a plant arose which produced some few ligulate florets in the midst of the disc. This indicated the production of a double race. When the seeds of this mutating individual were sown, the next year, they yielded a uniformly double group; and from this time the new variety remained constant.

The Dracocephalum moldavicum is an annual garden-plant belonging to a genus in which Morren has described

Fig. 2. A. The toadflax (*Linaria vulgaris*). B, C. Its peloric variety. D. A peloric flower on an ordinary specimen.

Fig. 3. A. The double-flowered corn-marigold (*Chrysanthemum segetum plenum*), an experimental mutation produced at Amsterdam, 1899. B. A flower-head of the original cultivated variety C. The first result of selection. D. The first sign of doubling. E. A typical double flower-head.

some beautifully twisted specimens. I succeeded in procuring such a specimen in this species by cultivating a race of it during some few years, selecting the specimens which showed a marked tendency toward variation in the arrangement of their leaves. The twisting appeared at once, but the race has not been continued.

All these, and many other, experiments have been conducted under conditions which allowed of a close scientific study. They confirm the common experience of the horticultural breeder in stating the suddenness of the changes and the immediate production of distinct races. They show us the way in which analogous changes may have occurred in nature, and make it probable that sudden changes are, at least, an important factor in the evolution of the vegetable kingdom.

With agricultural crops my experiments have been too rare to give a definite result. The German breeders assumed, as a rule, that they produced their races at will and by a process of slow variability and repeated selection. It is mainly upon this conviction that Darwin has based his conception of an analogous slow improvement of species in nature. This German method, however, has been submitted to a severe criticism by Dr. Nilsson, the director of the Swedish agricultural experiment station at Svalöf. His pedigree-cultures have shown that the idea of a slow accumulation of characters by repeated selection is due to incorrect observations and to the use of untrustworthy methods. According to his experiments, changes occur in agricultural plants as suddenly as in horticultural species; there is no essential difference between them in this respect. By these discoveries the main support of the theory of slow and gradual evolution is broken down, and the analogy between artificial and natural production of species comes to plead wholly for the theory of mutation. These new

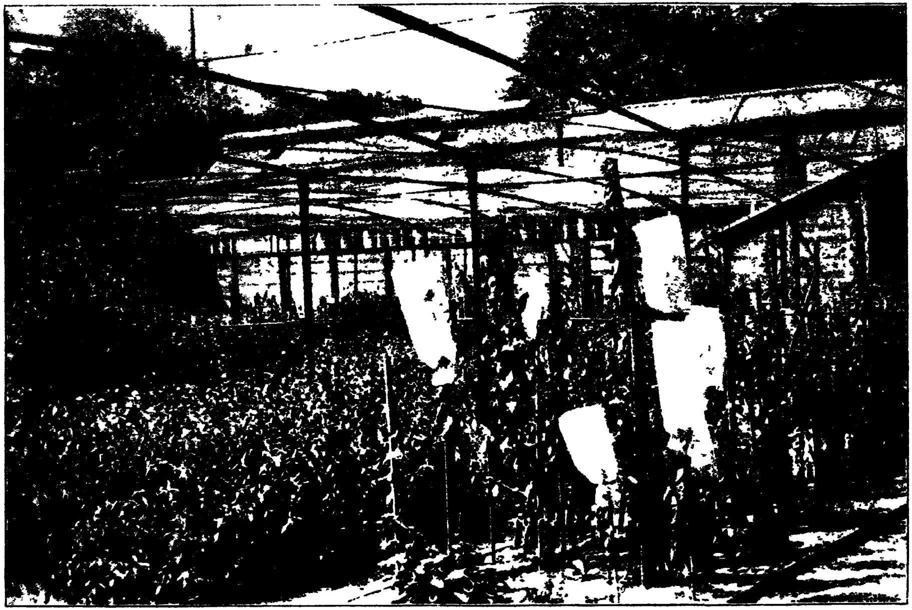


Fig. 4. The Experiment garden in the botanical garden at Amsterdam, covered with iron wire netting. Cultures of different Evening Primroses, some enclosed in bags for artificial pollination, 1904.

facts will be dealt with in our next chapter, and it may be sufficient, here, merely to have indicated them.

The principle of mutation is conducive to the assumption of distinct units in the characters of plants and animals. Even as chemistry has reached its present high development chiefly through the assumption of atoms and molecules as definite units, the qualities of which would be measurable and could be expressed in figures, in the same way systematic botany and the allied comparative studies are in need of a basis for measurement and calculations. The determination of the degree of affinity now largely depends upon vague estimates and personal views; while, on the basis of the theory of mutations, the relationship is measured by the number of the mutations which have made the forms under consideration different from their common ancestors. The mutations themselves have evidently occurred in previous times and cannot be counted now. But if it were possible to count their products, the characters, the same aim could be reached.

The study of these unit-characters may be undertaken in three different ways: first, by the production of hybrids; secondly, by the investigation of associated characters; and in the third place, by the direct observation of mutations producing such units. In hybrids the characters of the parents may be combined in different ways, but the unit-characters connot be split or divided. This follows directly from their definition. Thus the different combinations may lead to the distinction of the constituents of the mixture. In my third chapter I shall deal with this question on the ground of the experiments of Luther Burbank. They afford a sufficient source of evidence to discuss this question and are well deserving of a separate treatment. On the other hand, their methods and scientific results are the same as those of the European horticultural breeders, as described elsewhere.

Fig. 5. Lamarck's Evening Primrose (*Oenothera Lamarckiana*), a mutating species.

The association of characters is often called correlation. It may be an accidental or a normal coincidence of character-units. But more often the same simple character manifests itself in different parts of the organism (as, for instance, in the color of flowers, berries, seeds and foliage) and thereby affords a means of investigating it. Of late, such associations have become of high importance, since selection may be guided by them. Especially, in the isolation of new varieties of cereals has this use proven very valuable. Our fourth chapter will deal with these questions.

For the direct observation of the process of mutating, the evening primrose of Lamarck affords, at present, an unequaled opportunity. It produces numerous mutants, and does so in every generation, and almost any sample of pure seed may be used for this study. This species was described by Lamarck, from specimens of the botanical garden at Paris, a century ago. It seems to have since been lost. It was re-introduced into European garden-culture, about the middle of the last century, by a nurseryman in London, who received the seed, without name and in a mixed packet, cultivated and multiplied it and sold it to the leading firms on the continent. All the strains derived from this scource show the same phenomena of mutability, as far as my experiments go. Where the species is growing in America in the wild condition, is not known, at present, and so it is impossible to decide whether it has acquired the habit of mutating in that condition or upon its introduction into European culture.

Twenty years ago, I found this species on a waste field near Hilversum, in Holland, where it had escaped from cultivation and was rapidly multiplying itself. Here it had produced two new and distinct varieties which, up to the present time, have not been collected or observed elsewhere. One of them had smooth leaves, lacking the bubbles of the ordinary form; it was a fine type with narrower leaves and petals,

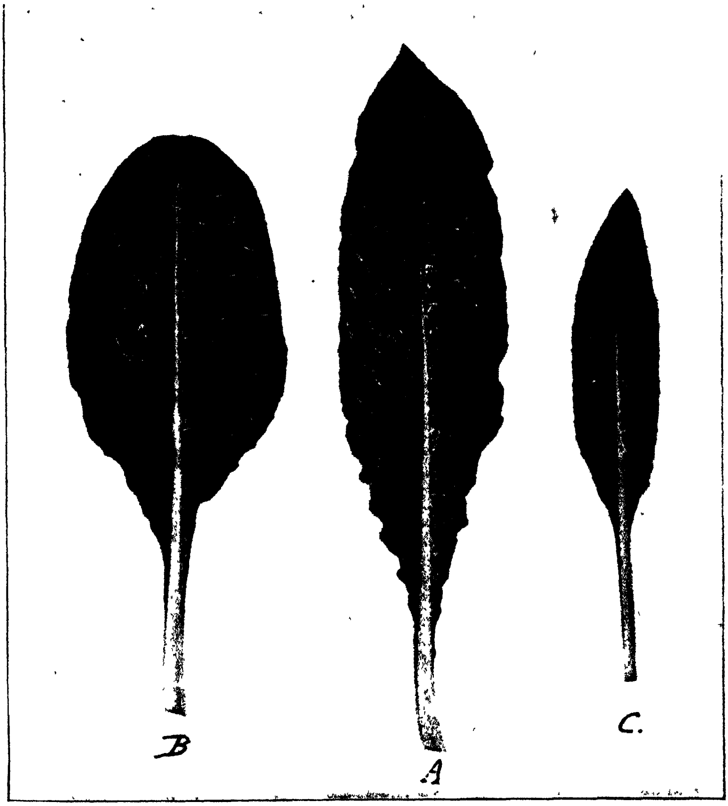


Fig. 6. Leaves of Lamarck's Evening Primrose (A), and of two of its mutants. B. *Oen. lata.* C. *Oen. scintillans.*

the latter often becoming ovate instead of cordate. The other had very short styles, the stigma reaching only to the mouth of the flower-tube, instead of being lifted up above the anthers. Its ovary is only partly inferior, and it ripens only very few seeds in its capsules, which remain small. It has, moreover, some associated characters in its foliage by which it may be recognized before the flowering-period. In my cultures, both these varieties were found to be constant and pure from seed. Some further mutations have been produced on the same field, but since they were also produced in my experiment-garden, I shall not here mention them separately.

In the year 1886, I collected some seed from the normal plants of this field and sowed them in my garden the next spring. This culture at once gave a new mutation wholly unobserved until that time. Three individuals diverged from the average, and all three in the same way. They constituted a new type which has been called Œnothera lata or the broad-leaved evening primrose. Its leaves have rounded tips, its stems are weak and bending and scarcely reach half the size of those of Lamarck's primrose. It has thick flower-buds and produces flowers the petals of which often cannot completely flatten themselves. The anthers are barren of pollen, dry and twisted. Its ovary, however, is normal and can easily be fertilized by the pollen of the parent species. In doing so the next generation is, of course, of hybrid origin, but it does not produce intermediates but consists of some typical Œnothera lata and some normal Œnothera Lamarckiana. By repeating the cross the lata type may be kept indefinitely, occurring in about the same numerical proportion in each generation.

Starting from these mutations, I began a regular scientific pedigree culture of Lamarck's evening primrose, fertilizing the flowers artificially with their own pollen, protecting them

Fig. 7. Mutants of the Evening Primrose. A. The red-veined form (*O. rubrinervis*), which is of the same size as the original species. B and C. The dwarfish variety (*Oen. nanella*).

from the visits of insects by paper bags and sowing, each year, the seeds of some few normal individuals of the race This pedigree embraces, now, about a dozen generations, the first few of which were biennial, but the later annual. From this stock of normal plants it has regularly repeated its first mutation, producing some latas in almost every generation. The number of these mutants was, on the average, about 1½ per cent, the mutants themselves being always alike.

Moreover, my pedigree culture has produced quite a number of other mutants. The most frequent among them is a dwarfish variety, the first flowers of which open when the stem is only some few inches high. It is called Œnothera nanella and occurs as frequently as the Œnothera lata. It is completely fertile and produces an abundance of seeds, all of which give the same dwarf type, without ever reverting to the high stature of the parent species. I have cultivated these dwarfs during five, and more, generations and have found them true to their type.

The first generations of my pedigree culture had to meet with all the difficulties of a new experiment with unknown and partly unsuspected results. Accordingly, they yielded only a small number of mutants. As soon as the method had been elaborated, this number rapidly increased. In the spring of 1895 I sowed seed enough to have about 14,000 young seedling plants, which I cultivated until they clearly showed whether they would mutate or not. The mutating individuals were than isolated and grown under very favorable conditions, but of the normal plants the larger part were destroyed. All in all, I isolated 60 dwarfs and 73 lata and five wholly different new types. Two of them were rare, one having been found only in one (O. gigas)and the other in two individuals (O. leptocarpa). Two others were less rare, the rubrinervis appearing in eight, and the albida in fifteen specimens. The fifth was the most frequent of them all, spring

Fig. 8. A flowerspike of the giant mutant (*Oenothera gigas*), which originated in my garden, 1896.

ing from the main stem of the Lamarckiana in 176 of the 14,000 seedlings. It was called oblonga. All these forms were purely self-fertilized and yielded uniform races without reversion to the original evening primrose of Lamarck.

With the exception of the gigas, which has not been repeated in this pedigree, all the types spring more or less regularly, in every generation, from the pure parent stock. As often as they were purely fertilized they produced constant strains, which, however, did not differ from the previous races of the same name.

Besides these, quite a number of minor mutations have occurred in my cultures. Some of them died in early youth or before flowering; others were barren of pollen, or not capable of fertilization, and yielded no seeds. Some were too weak for the conditions of my garden and succumbed, sooner or later, mostly during the winter after their germination. The range of mutability of this primrose, evidently, has not been exhausted; and even during last summer a wholly new type made its appearance.

A main point in these observations is that the mutations occur suddenly, without preparation and without intermediates. Nothing indicates on the normal plants what their seeds will produce, and there is even no means at all by which to decide beforehand whether the fruit of one individual, or one branch, will be richer than any other in the production of mutations or of some distinct mutant. The distribution of mutating seeds seems to depend simply upon chance. Nor are there intermediates. Each mutant is as good a representative of its type as its progeny will be; it does not need any special cultivation or improvement to reach the full display of its character. No half-mutants are seen, neither from seed of the parent form nor from seed of the first mutant itself. These sharp distinctions clearly indicate that each mutation consists of the production of a single unit-

Fig. 9. A flowerspike of the red-veined mutant (*Oenothera rubrinervis*), which has been produced almost yearly by the parent species.

character; because, if the characters were compound, they would split, from time to time, and be divided into their constituents. By this means a method is given of studying the expressions which the same unit-character may assume in the different organs of a plant. But this point will be more closely studied in another chapter.

The question now arises, whether it must be supposed that species in nature ordinarily originate in the same way as in the case of the evening primroses. Of course, the details of the process will be different in different cases. The number of the new types and the frequency of the mutating individuals in each will differ; sometimes they may, perhaps, be more rare and, in other instances, more crowded. Other differences there will be, also. The main point is, however, that mutations occur suddenly and by leaps. One generation is sufficient to produce the whole new type. This is a manifest contrast with the prevailing conception of slow and almost invisible changes producing new species. It may shorten the geological time required for the evolution of the whole living world and bring it within the limits derived from physical and astronomical evidence. Thus the theory of mutation satisfies these demands.

The cases observed in horticulture, the constancy of wild species, the behavior of characters in crosses, the occurrence of sharply defined small species within the ordinary species of wild plants and even of agricultural crops, and many other groups of facts, lead to the same conclusion. On the other hand, the slow change of one species into another has not, as yet, been proven in any distinct and clear case. Therefore, we may assume that the mass of the present evidence points to the conclusion that species originate laterally from other species, by sudden leaps. These leaps we call mutations.

Fig. 10 Dr. Hjalmar Nilsson, Director of the Swedish Agricultural Experiment Station at Svalöf.

II.

THE DISCOVERY OF THE ELEMENTARY SPECIES OF AGRICULTURAL PLANTS BY HJALMAR NILSSON.

A. DIFFERENT PRINCIPLES IN THE BREEDING OF CEREALS.

From the beginning of civilization, the cereals have taken a prominent place in human culture. No industry has been so intimately connected with the interests of mankind, and upon no other agricultural crop has progress been so largely dependent. Long before the time of the ancient Egyptian kings, of the Romans and of the lake-dwellings of central Europe, the cereals yielded the principal nourishment in all the countries of the world where civilization developed itself. Solms-Laubach has pointed out that China and Egypt have cultivated mainly the same species and sub-species of grains, and that on this ground it must be conceded that their cultures have had a common starting-point. Three or four thousand years before Christ, the principal varieties must have been known to mankind, and it may even be assumed that the very first beginning of this culture is much older. Its probable origin is the central part of Asia, since only this region can have been its common source for the Chinese and Egyptians.

Having so deep a significance, the cereals must have been given more attention and more care than any other crop. According to some verses of Virgil, the Romans knew their cultivated races to be far from pure and uniform. They also knew that care had to be taken in the harvesting of the grains destined for sowing, since otherwise the races would surely deteriorate. Each year the best ears had to be selected in order to keep the varieties pure from an overwhelming

Fig. 11. Poland wheat (*Triticum polonicum*).

increase of the unavoidable admixtures of little worth.

During the middle ages no records seem to have been made as to the methods of cultivating cereals. Wheat and barley had been the grains of the ancients; to these, oats have been added during the period of the lake-dwellings, and rye is the most recent of the European species, having been introduced into Europe during the middle ages. Corn, of course, is of American origin, and has been connected with the development of the ancient American cultures, quite in the same way as the grains were connected with those of the old world.

The idea of improving these valuable crops seems to have presented itself only after the beginning of the last century. Different principles were set forth, as soon as the possibility of improvement had once been ascertained. Some of them were of a more practical nature, resting on direct observation, but others relied on theoretical views concerning the influence of environment on the qualities of living organisms. Both of these main directions have attained a high degree of significance in agricultural practice as well as in the purely scientific discussions concerning the origin of species in nature.

English breeders have, as a rule, preferred the more practical line of working, but their results have been isolated, and have not been combined into a definite system. German breeders, on the other hand, have followed the theoretical principle of slow amelioration, and have developed this idea into a broad system, which has been applied by several of their most prominent men to the improvement of numerous varieties.

Darwin, as is generally known, chose the principle of slow and gradual changes as affording the most reliable facts for his discussion of the manner in which species are produced in nature. In doing so, he has brought the German method to the rank of a scientific principle and secured for it the interest of the students of biology at large, but has almost thrown into oblivion the other side of the question.

Of late, however, new facts have been discovered, which are of a nature to change the whole aspect of this part of the science of evolution. At the Agricultural Experiment Station of Sweden, at Svalöf, the German method has been extensively tested, and the result has not been favorable to it. New discoveries have been made which go to prove that the whole principle of gradual changes rests on an insufficient knowledge of the laws of variability of agricultural plants, and may be replaced by more simple and more direct methods as soon as these laws are exactly studied. It is my object to give a survey of the deep significance of these Svalöf experiments, partly in their practical bearing on agricultural plant breeding, but mainly in their complete compliance with the doctrine of elementary species, and in their appreciation of these as the true material from which selection has to make its choice. I shall endeavor to point out that these new discoveries must deprive the principle of gradual ameliorations of its present high rank in agricultural practice, as well as of its significance as a support for the prevailing views concerning the origin of species in nature.

Before doing so, however, an historical sketch of the principal methods and achievements of the most renowned breeders of cereals may be given. It will facilitate our

Fig. 12. A. Bellevue de Talavera-wheat, isolated by Le Couteur. B. Bearded white wheat, produced by Patrick Shirreff. C. Squarehead wheat, the most famous production of the same breeder.

appreciation of the most essential features of the wonderful variability of these plants, and will prepare us for an unprejudiced judgment of the opposite views concerning the

significance of different kinds of variations for breeding experiments and for scientific discussions.

The first to discover the principle of improving cereals by selection was the English breeder, Le Couteur. He lived in the first part of the last century on Jersey, one of the islands in the Channel, off the coast of France. Once he was visited by Professor La Gasca of the University of Madrid, who, far from admiring the purity and uniformity of his host's cultures, pointed out to him how, in reality, they consisted of a mixture of more or less easily recognizable types. He suggested the idea that these types might have a different share in the harvest of the whole field, some of them being probably more and others less productive than the average. In a field of wheat, he succeeded in distinguishing 23 forms, and in other cultures similar indications of variability were observed. After his departure, Le Couteur saved the ears of the indicated types separately, and sowed their grains in small field plots in order to compare their productivity. He does not seem to have had any theoretical view concerning the causes or the nature of the observed differences, but simply assumed that the progeny of his selected plants would be like the parents. On this point he soon found himself justified by the results of his experiments. He had produced a group of new types of which some proved better and others less valuable than the ordinary sorts of his fields. The best new varieties, isolated in this way, he then multiplied, and afterwards put them upon the market. One of them is still grown in England and the northern parts of France on a tolerably large scale. It is a kind of wheat called "Bellevue de Talavera" and it is known to be a very pure and uniform type. It is so uniform that it does not afford any deviations by which it can be subjected to further selection, and all trials in this direction have been in vain. Many breeders of later times

have approached this high degree of invariability in the products of Le Couteur's selection, and only at present is it recognized as an instance of one of the most common laws, which rule the phenomena involved.

Another celebrated breeder who worked on the same principle, though after a somewhat different method, was the Scottish agriculturist, Patrick Shirreff. He lived in about the middle of the nineteenth century and had his farm at Haddington in Haddingtonshire. During the first period of his work, he had no better conception concerning the purity of his fields than his contemporaries. But he observed that, from time to time, and as he thought by mere accident, a plant occurred which seemed far more promising than all the remainder of the same field. Such individuals he marked, helping their development by pulling out their neighbors if they were crowded and surrounded them by all manner of attention. Then he saved their seeds separately and sowed them, in order to multiply his new types as fast as possible. That such isolated individuals would yield a uniform progeny and become the ancestors of constant races he took for granted, and it is very curious to note in his writings that he did not judge it worth while to discuss this point, or to state the fact as he observed it. His races were pure, and there was no single reason for him to suggest that it could have been otherwise.

Shirreff's exceptional plants were very rare, so rare even that in the first period of nearly forty years, he succeeded in isolating only four new varieties of prominent value. His first discovery was made in the year 1819. He observed a plant of wheat which surpassed its neighbors by its high degree of branching. It yielded 63 ears with about 2500 kernels. He saved the seeds, sowed them on a separate field and at considerable distances apart so as to induce in all the plants the same rich branching. He contrived to

multiply it so rapidly that it took only two generations to get seed enough to bring it advantageously into the trade. He gave it the name of Mungoswell's wheat, and it soon became one of the most profitable varieties of Scotland. It has found its way into England and into France, where it is still considered one of the best sorts of wheat.

It is interesting to note that Shirreff had no idea of the necessity or even of the usefulness of a repeated selection. On this point he wholly agreed with Le Couteur. Without exercising any choice, he sowed all the grains of his selected plants and of their progeny, his only aim being to multiply the new form as quickly as possible. They yielded a uniform race, and were simply expected to do so.

Only five years after his first selection, another exceptional plant caught his eye. It was an exceedingly tall individual in one of his fields of oats. He saved and sowed its seeds separately as in the previous case and won a variety which has since been largely cultivated under the name of Hopetown oats. His remaining varieties were the Hopetown wheat, found in 1832, which was discovered and multiplied in quite the same way, and the Shirreff oats, concerning the origin and treatment of which he has not judged it worth while to give any indications. Both of them have gained a high reputation and a widespread culture in Scotland as well as in some other European countries.

Until the year 1856, these four varieties were his only improvements. At that time, however, he had acquired more experience concerning the variability of his cereals, and he resolved to profit thereby. He had observed that though exceptionally promising plants are of course very rare, less promising individuals may be met with in larger numbers. They would not yield such excellent races as the four mentioned above, but notwithstanding that, they might suffi-

ciently surpass the average to be advantageously selected and cultivated. The trials would have to be made on a larger scale, and the results would be less striking, but on the other hand, improvements could be brought about in a far lesser number of years. Or, to state it more correctly, the results would no longer be dependent on rare and casual discoveries, but would be brought about systematically.

He began his selections, after this new method, with wheat, and saved 70 ears from different individuals. All of them seemed to promise more than the average varieties of his fields. Of course the kernels were sown separately for each mother plant, and their progeny was accurately tested and compared. As previously, he took it for granted that all of these new strains would be constant and uniform; he observed the fact but did not judge it interesting enough to mention it specially. Among his 70 strains he chose at the end the three best ones, multiplied them as fast as possible in order to bring them into the trade, and rejected all the others. Those three received the names of Shirreff's Bearded Red Wheat, Shirreff's Bearded White Wheat, and Pringle's Wheat. For many years they have had a notable place among the best local varieties, and the white variety among them has even found its way into England and France.

Having obtained these results with wheat, he started, in the year of 1862, a similar experiment with oats. Four of his selections proved to excel the common sorts and were introduced into the trade. They bear the names of Early Fellow, Fine Fellow, Long Fellow, and Early Angus. Like the wheats, they have been constant and uniform from the very beginning.

Ten years afterward, Shirreff published an account of his results and of his methods. It was a little book, printed only for private distribution. But it has been translated

into German by Dr. Hesse for the use of the general public. It is largely devoted to the description of the superior qualities of his varieties, and the historical evidence concerning their origin is only incidentally given. From his statements, we may gather that at first he assumed his mother plants to be sports, but afterwards took them to be simply old constituents of the ordinary cultivated varieties. He observed these to be mixtures, consisting of more and of less abundantly yielding types, and on this observation founded the method which he followed during the latter part of his life. He satisfied himself that even within these mixtures the constituents were uniform and constant races, and therefore it was only natural that after isolation they would remain so. Shirreff seems not to have had any idea of the possibility of the existence of another form of variability as a starting point for further improvement. Considering the great importance which has been conceded in Germany to this possibility, even during the latter part of Shirreff's life, it is not without interest to lay some stress on this fact. The more so, since he had in mind the desirability of other ways to reach the same purpose more surely and more quickly. He turned himself to hybridizations and made some valuable experiments on the crossing of cereals, and from his statements it seems quite evident that he did so only in the firm conviction of having exhausted the possibilities offered him by variability alone.

Le Couteur and Patrick Shirreff seem to be the only breeders of cereals who have worked on the principle of one single initial selection and of subsequent rapid multiplication without renewal of the choice and without isolating the best individuals during the following generations. On this point they are to be considered the precursors of the method which has of late been discovered anew, at Svalöf. But they had only a very limited appreciation of the importance

and productiveness of the principle involved in their method of selection.

At nearly the same time with the latter experiments of Shirreff, another renowned breeder began to improve cereals by selection. At Brighton, in one of the southern districts of England, F. F. Hallett began his work in the year 1857. He seems to have known the improved varieties of Le Couteur but not those of Shirreff. He started from quite another point of view, which did not rest upon the observation of the variability of his grains, but was derived from his previous experience in the breeding of cattle, especially in that of the short-horns.

His principle was that each plant has one head which is the best of all its ears, and that in the same way each ear has one best kernel. Moreover, he was convinced that the best kernel of the whole plant is always to be found in the best ear. He also assumes that the qualities of the single kernels are inherited by the plants which they produce. From these premises he concluded that varieties could be improved by choosing the best kernel of the best ear for their reproduction. This choice had to be repeated through a series of generations, but his experience taught him that though the gain was large in the beginning, it did not continue so, but soon reached a limit which it was practically impossible to transgress.

Two other features distinguished his work from that of Le Couteur and Shirreff. In the first place, he tried to improve his plants directly. He satisfied himself that a plant, in order to attain its utmost development, must have ample food at all seasons, and that for this purpose not only manure but also depth of soil and space were essential. Therefore he planted his selected plants in a little garden near his house, gave them the best garden soil and the ordinary culture and treatment of garden plants. By this

Fig. 13. A. Hallett's pedigree Chevalier barley. B. Hallett's pedigree wheat.

means he increased the number of their culms and heads and the number of the spikelets and kernels in the individual ears. Twenty to fifty and more ears on a plant of wheat

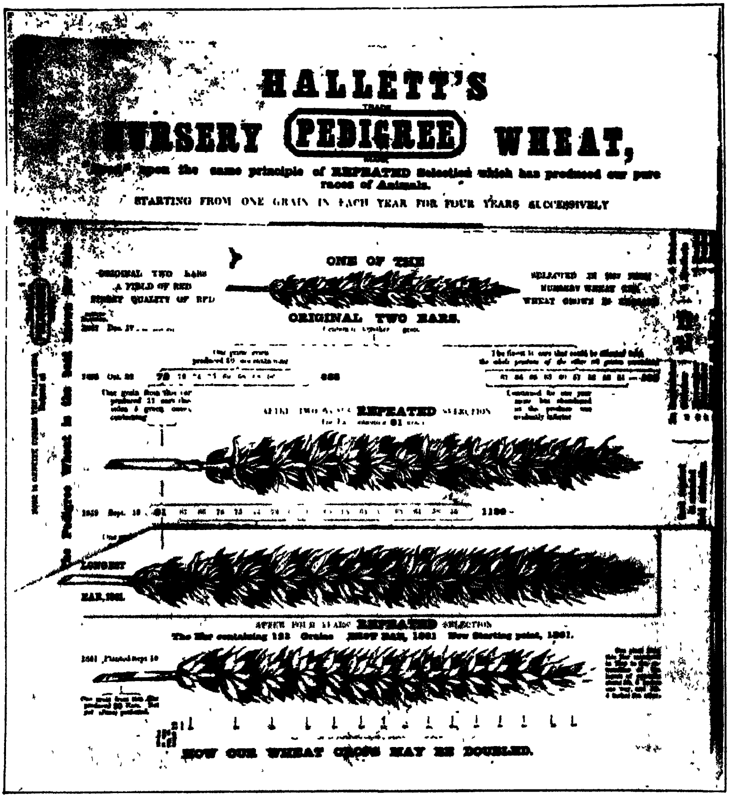


Fig. 14. A reproduction of part of the first advertisement of pedigree wheat by F. F. Hallett. See the *Times*, London, June 18, Nov. 8, and Dec. 19, 1862.

became the rule, and ears with less than 80–100 kernels were commonly rejected. This large increase can in some sense be called artificial. It appears as a direct result of the change of culture and therefore came wholly or almost wholly during the very first year of the selection experiment.

Of course the influence of better nourishment can only attain its highest degree in the lapse of some generations, since only the very best nourished kernels will yield the very richest plants. In some cases, this process of artificial amelioration will be rapid, but in others more or less slow. Some instances may be given. Hallett's "Original Red Wheat" was started from an ear containing 47 kernels. The next generation yielded an ear of 79 grains, and the second came up to 90 in the richest ear. During the seventeen following generations, this limit has practically not been exceeded, the richest ear during all that time having produced only 91 kernels. In other cases the development was equally rapid in the beginning, but lasted during a longer period. The Hunter's Wheat began with 60, increased in the first year to 90, and then during some twelve years came up to 106 in the best ear. The Victoria Wheat began with 53 and slowly increased to 101, the gain of the first generation being only seven kernels for the best ear. Hallett assumed that by this treatment the hereditary qualities were affected in the same way as the visible characteristics, or in other words, that the varieties were directly improved by the culture, the selection having only the purpose of fixing the acquired qualities.

A second feature of Hallett's method was the great care bestowed by him on the comparison and testing of his plants. For each single individual, the heads were counted and the exact number of kernels in each ear traced. These figures were considered as the main qualities according to which the plants were judged, and on this ground the average specimens and those of minor worth could be eliminated. The prominent ones were then brought to his study and minutely compared in all their visible marks. In this way the very best specimen was isolated, and the same work begun for its culms and ears. Only one ear was ultimately

chosen for the sowing of the next generation, and this was the best on account of its having not only the largest number of kernels, but also the biggest and best formed ones of them all. Repeatedly Hallett has insisted upon the immense amount of work which this kind of selection yearly required. This is the more curious since at the present time hardly anybody attributes much importance to a choice of the best seeds on a given individual, provided only that small or unhealthy kernels are sufficiently excluded.

For Hallett, on the contrary, the choice of the one best kernel on the whole plant was the real aim in his selection. He tried all means for comparing the individual kernels of his one superior ear with one another and for finding out the best one. He made investigations embracing, on one side, their visible marks, and on the other their places on the ear, those in the middle part being in the main the better ones. But he could not discover distinct laws and so had to give up the whole system. Leaving aside all comparison of the kernels of his chosen head, he resolved to sow them all and to delay their study until the next generation. In this he repeated his testing in the manner described and judging the kernels from the plants they had produced, he was enabled to discern among them the one by means of which he wished to continue his race.

To this method of selecting each year the best kernel on the best ear of the best plant, Hallett has given the name of pedigree-culture. Its essential feature is the repeated selection. Some of his varieties were given to the trade under the names of pedigree wheats and pedigree oats. Of the latter, his "pedigree white Canadian oats" and his "pedigree black Tartarian oats" may here be mentioned. Both were introduced in the year 1862. He claimed that his gradual amelioration gave better varieties than the principle of the isolation of single plants. This may be seen by

the title of the address delivered by him in London in 1862, in which he first published his results and his views. It was entitled, "On pedigree in wheat as a means of increasing crop." The improvement was obtained by the increase of the size of the ears, their number of kernels and the size of the latter. The number of heads on a plant he did not consider as a subject of selection, but rather assumed that it was wholly determined by the relative distance between the plants and therefore by the space given them in sowing. For him, the productiveness of a field was proportional to the yield of the single ears.

Moreover, he assumed that his pedigree-races were not only to be ameliorated but must be kept up to their highest point of development by continued selection. As soon as selection ceased, they would return to their original starting point and their superiority over the ordinary cultivated varieties would disappear. This assertion has a distinct and deep significance in agricultural practice, and has gained a great deal of influence in the discussion of theoretical questions as well. For practice it means that all the seed destined for sowing should be produced directly from the pedigree-stock, and that this is to be kept constantly under the same conditions of treatment and sharp selection. The truth of this assertion has been accepted by his customers, and this fact has left the production of seed grain almost entirely in his hands. It is easy to see that the gain made by the breeder of a new variety depends, for a large part, on the acceptance of this proposition. In the varieties produced by Le Couteur and Shirreff, all seed is of equal value, provided the races are kept pure and free from admixture. Any one may multiply them with the same success as the original breeder, but on Hallett's principle all the profit of the production of reliable seed grain was given into the hands of him who kept the original pedigree.

I need not now discuss the truth of this assertion, since the same principle has been accepted by the German breeders. I might, however, point out that the real difference between Hallett's method and that of his two previously mentioned countrymen is to be sought in the choice of the starting points of their experiments.

Le Couteur and Shirreff have expressed themselves clearly on this point. With them, all depends upon the first choice. What remains to be done afterward, is only the multiplication of the progeny of the chosen plant. Hallett, on the other hand, is silent on this most essential question. Like them, he started, in each single case, from one plant, and therefore must have made a choice among the types which his fields afforded him. On Shirreff's conception, this choice must have been the decisive point in Hallett's work, and not the subsequent selection, and that this is true may be proven by his arguments. In the first place, Hallett has brought into the trade new and distinct varieties, and not merely more productive strains of the ordinary sorts. This may be seen by the names of the forms already cited, and to which the very distinctive types of his Golden Drop wheat and Chevalier barley may be added. Moreover, it is proven by the fact that his varieties have kept their place in agriculture at large and are still keeping it, although it is a long time since Hallett himself discontinued their pedigree-culture. They are now known to be independent varieties like those of Le Couteur and Shirreff.

A second argument is given in the fact that the value of Hallett's varieties is dependent on his first choice, and that if this should prove a mistake, no subsequent selection is adequate to amend it. The proof of this is given by the miscarrying of some of his pedigree-cultures. Of course, most of these cases he will hardly have mentioned, but it is

a well-known fact that his "Original Red Wheat" afterward proved to be a failure.

A very remarkable principle has been introduced of late into the methods of improving cereals by two highly distinguished breeders. Working independently of one another, they have come to the same idea, and the ameliorations they have brought about give proof of the correctnessof their views. At the agricultural experiment station of Minnesota, W. M. Hays has applied it to the improvement of wheat, and in Germany on his farm at Petkus von Lochow has applied it to the selection of rye. The idea is the judging of the hereditary value of a plant, not by its own visible marks, but by the average value of its progeny. It must be granted that the visible qualities of a plant are only a very imperfect basis of measurement of its fitness to reproduce these qualities in its progeny. The direct study of this progeny in itself must be a far more reliable guide in such an estimate.

The new principle was of course combined with the choice of single parent plants as the starting points for new races, and in this important feature it complies with the principles laid down by the two first English breeders whose methods I have discussed. But with them the first choice was the principal act, although Le Couteur as well as Shirreff in his second method have largely relied on the comparison of the progeny of their first selections and rejected all those that proved inferior to his expectations.

In Minnesota, the most widely cultivated varieties of wheat were Fife and Blue Stem, and both were decidedly inferior to the ordinary spring wheat varieties of other states. However, they showed themselves to be as impure as any other ordinary sorts, and thereby yielded material for methodical improvement. Hays chose from among them a considerable number of types, and after sowing the seed of these

single mother plants, he compared their yielding capacity in the next generation. In order to have an easy standard of comparison, he sowed a hundred kernels of each and thence derived the name "centgener power" for the index of productiveness of the single races isolated in this way. He claims to have obtained varieties which, under the same culture and treatment, will yield 10 to 15 per cent more than the old unpurified wheats of Minnesota.

The same principle of judging the parent plant by the average value of its progeny, and of founding selection on this mark, has been applied by von Lochow to rye, and it is said that his new race of "Rye of Petkus" as it is called, excels all the older improved German kinds of rye, and that even the celebrated rye of Schlanstedt may soon prove to be surpassed by it.

We have given a survey of the most prominent and most renowned principles in the breeding of cereals, and have only to complete our list by a description of the method followed by the larger number of the breeders of Germany. Among them, Heine, Drechsler, Mokry and Rimpau may here be named. Their purpose was to improve the ordinary varieties by continuous selection, directed according to distinct views and requirements. They considered the starting points of the English breeders as accidental sports which no doubt might be made use of with advantage, but would only yield improvements of an inferior rank.

Two features are essential to this German method. First the initial choice, and secondly the slow and gradual improvement by selection. In this first choice they did not try to obtain deviating types and to isolate them from among the throng. Quite on the contrary, they selected the best representatives of the variety they wished to improve, in order to be sure to retain all of its good features in the new race and to combine them with the new characters which

they thought it possible to give them. Starting from this point of view, it was essential not to begin with one single mother plant, for this might perhaps possess, among those qualities which necessarily or at least ordinarily escape observation, some inferior ones, which, it must be feared, might destroy the whole effect of the ameliorations obtained on other points. Dependence on soil and manure, resistance to disease and other essential qualities are not so easily taken into consideration when the selection is performed only at the time of the harvest, as was then the custom. In order to become as independent of these as possible, the only way seemed to start with quite a considerable number of individuals and to rely on the laws of chance, trusting that these would keep all qualities in their average state, except those which should be consciously subjected to selection. It was this group of individuals that was to be ameliorated. A scheme of the desired improvements was made, and each year those ears or panicles were selected which more fully complied with it than the remainder. The result was a slow progress, but it was thought to be more reliable than the sudden amelioration of the English breeders. Moreover, sudden improvements are, as a matter of fact, limited in their degree, and even the pedigree-cultures of Hallett did not escape from this objection. The German principle was assumed to be unlimited, progress along the prescribed lines seeming to be always possible.

As pointed out in the beginning, Darwin has, in large part, founded his theory of the slow and gradual change by which the species of plants and animals are transformed into one another, on the views of the German breeders of his time. For this reason we shall have to subject their principles to an elaborate criticism and the short indication given may therefore be sufficient for our present purpose.

The most general conclusion to which our historical

sketch has led us is obviously that by very different methods and under the influence of widely divergent theoretical premises, equally good improvements have been obtained. We may add that even in the number of new and useful varieties produced, no single one among these methods evidently excels the others. It is always a small number, not exceeding ten or perhaps twenty novelties in each single instance, and ordinarily even far less. Thus all these principles are seen to have only a limited application, and perhaps failures have been more numerous than successes although as a rule only the latter have been recorded. Hence we may conclude that our knowledge of the variability of cereals is not yet sufficient to enable us to exhaust all of its possibilities, or at least that such a knowledge was not in the possession of the breeders whose great achievements have given the material for our present sketch.

B. THE SWEDISH AGRICULTURAL EXPERIMENT STATION AT SVALÖF.

During the last twenty years, experiments in the breeding of cereals and other agricultural crops have been conducted on an unusually large scale at the Swedish experiment station of Svalöf. Considered from a practical point of view, they have produced quite an astonishing number of new races, by which agriculture in almost all the districts of Sweden has been greatly improved, and which are now attracting the attention of numerous agriculturists in other countries. Their methods took their origin from those followed in Germany, but were soon changed, and may, at present, be more closely compared with the work of Le Couteur and Shirreff, though developed quite independently of these men, whose ideas were, at that time, only locally appreciated.

For the students of the problems of evolution, the methods

Fig. 15. The Swedish Agricultural Experiment Station at Svalöf. Part of the campus and residence of the Director.

and the results of the Svalöf station have a very deep significance. They confirm the fact that the ordinary cultivated varieties of cereals are by no means pure, but must be considered as mixtures of well defined types. Moreover, they show that these types are far more numerous than was previously supposed, and include hundreds of forms within each of the now prevailing sorts. They also show that the differences among these newly discovered elementary types are far greater than might be suspected from the study of the varieties isolated by other breeders. The range of variability disclosed by these new studies is simply so wide that it affords all the required material for almost all the selections desirable at present, and will no doubt continue to be an inexhaustible source of improvements for a long succession of years. They are founded on the principle of single selections, and the range of application of this method is proven to be so extensive as to make all ideas of repeated or continuous selection simply superfluous. It is even so rich in its productiveness that there is scarcely any room left for other methods of improvement; and especially should all endeavors of winning ameliorated varieties of cereals by means of hybridization simply be left out of consideration, as compared with the immense number of more easily produced novelties which this method offers.

Leaving the teachings which may be derived from this work in the study of the evolution of the organic world for another chapter, I shall now try to give an idea of the work itself. This may be divided into two parts; the first comprising the use and criticism of the German method, and the second embracing the discovery and application of the principle of selecting elementary species.

Some historical details may precede this discussion. Svalöf is a little village in the Swedish province of Schonen, situated in the neighborhood of Helsingborg, Lund and

Malmö, close to the southwestern shore, and opposite Copenhagen in Denmark. In this village, a company for the production and improvement of seed-grains for the southern part of Sweden was organized in the year 1886. Its aim was the procuring and testing of new and foreign varieties of agricultural crops, in order to replace the Swedish sorts, which at that time were slowly but manifestly deteriorating. This deterioration was discovered to be a consequence of the multiplication of admixtures of less value, which, though rare and unobjectionable in the countries whence the varieties were derived, were seen to thrive in a most obnoxious way under the influence of the Swedish soil and climate, and to lessen the value of the harvest in an important degree. To procure new samples of seed grains was the first way of combating this evil, the second being the purifying of the introduced supplies before giving them into the hands of the Swedish farmers. This cleaning could be performed partly in the imported samples themselves, but had to be combined also with the culture and multiplication which usually precede the sale.

The company was founded by private agriculturists and had consequently to serve only the needs of practice. All educational aims and purely scientific researches are excluded from its program, but, on the other hand, its work is based on exact scientific methods. Its botanical studies are as broad as possible, but always in the direct service of agricultural practice. In this respect it is to be sharply contrasted with most of the experiment stations of Europe and America, and it is important to state that exactly through this procedure the obtained results have come to be of exceptionally great significance for science as well as for practice. Another consequence of this essential feature of the program is that its publications are destined only for the farmers of Sweden. They are published in the Swedish

language and deal with the results of the work. Fortunately, however, the Director and his staff have, from time to time, given short surveys of the progress realized, and of the methods followed in securing these practical results.

One of the means by which the young company contrived to gain a notable influence over Swedish agriculture, was by increasing the interest of the farmers in the purity and the control of their seed grains. Exhibitions and distributions of samples of pure seeds, descriptions of the various marks by which the varieties may be recognized, repeated inspections of the fields of the station, where pure cultures were grown side by side with the common Swedish sorts, gradually convinced the farmers of the great significance attached to the careful choice of their sowing-seeds. As soon as this conviction became general, the results could no longer remain doubtful, and, gradually, the fame of the station increased to a degree corresponding with the augmentation of the harvest.

This purification of the imported strains must evidently lead to an exact study of the constituents of the original mixtures and to a comparison of the part they take in the harvest. In the beginning, however, these were wholly obscured by the views which were then prevalent in Germany concerning the improvement of races among agricultural plants. It was taken for granted that the purification of the imported samples was simply to make them true representatives of the variety under the name of which they had been bought, so as to guarantee their quality to the Swedish purchasers. Furthermore, it was desired to acclimatize the best foreign kinds and to make them suitable to the requirements of the soils and climates of Sweden as well as to the various demands of the local industries. This part of the program, however, was intended as an application of the German

Fig. 16. The New Building of the Swedish Experiment Station at Svalöf, erected 1907.

methods of improvements to the special needs of Swedish agriculture.

From these statements it may easily be gathered that the importation of new and valuable kinds from neighboring countries was, at first, one of the chief occupations of the station. The most prominent and most renowned varieties of the cereals of Europe were purchased and tested, the old and common sorts as well as the newly introduced and ameliorated kinds. After finding them adequate to the local circumstances, they were multiplied, exhibited and recommended and finally given to the trade. In this way, Probsteier oats, Ligowo oats, Squarehead wheat, Victoria peas and different kinds of barley have been distributed. By their culture, the agriculture of the southern parts of Sweden was noticeably improved, and even the export of grains to Belgium and other European countries, which previously had suffered much from the deterioration of the races, could be restored to its former degree of importance.

The influence of these new methods may best be judged by the rapid growth of the company. Already in the second year, it could extend its interests, which were primarily intended for the southern part of Sweden only, to the whole country. Soon afterwards, another company was organized on the same principles and with the same aims. It had its seat at Orebrö and was destined to work for the middle part of Sweden. But after an existence of only four years, it was combined with the Svalöf company, which then (1894) took its present name of Sveriges Utsädesforening, or Seedgrain Society for Sweden. It entered into relationship with the greater number of local agricultural companies and was financially aided by them as well as by the Swedish government, so as to be enabled to work on a largely increased scale.

Gradually the combination of the experimental and the commercial sides of the work became too cumbersome, and

moreover brought about a kind of competition with the local seed dealers, which was felt to be a hindrance to its further development. Five years after its establishment (1891) these considerations led to a separation of the two branches, a separate company for the sale of the improved grains being organized under the name of Allmänna Svenska Utsädesaktiebolaget or General Seed-grain Trading Company of Sweden. This company has its seat at Svalöf, too, and receives the seeds of the ameliorated varieties which the society has produced, in order to multiply and distribute them. It is operated constantly under the control of the seed-grain society and thereby is enabled to keep its races uniform and to sell them under a full guarantee of purity.

Before leaving the history of the experiment station, some words should be added concerning its means of providing races for different parts of Sweden. Sweden embraces a wide range of climates, from its cold northern parts to the mild and favorable clime of the southern provinces. Moreover, there is a large variety of soils. Hence it is evident that the production of good cereals for all those various parts cannot be effected at one single point. No variety can claim to be appropriate for a definite soil or climate before it has been tested under the circumstances for which it is destined. The work of the society is therefore twofold, and the principle has been accepted that the varieties are produced at Svalöf, but afterward sent to other localities, according to their qualities and their probability of success. Everywhere in the country, the numerous local agricultural societies are co-operating with the station of Svalöf for this purpose. As soon as a new race is considered especially recommendable for some soil or some climate, it is sent to the locality in question and tested there by field cultures in comparison with the local sorts. By this means, many valuable improvements of local cultures have been obtained.

With the same object in view, two branch stations have been organized. One of them is situated at Ultuna in middle Sweden, and the other at Alnarp in the same region but on a richer soil. At Ultuna, for instance, the cultures of the new Svalöf Black Bell oats are attracting special attention.

During the first years of its existence, the station followed the methods of selection and amelioration which, at that time, were generally accepted by the breeders of central Europe. As we have seen in our last lecture, the German breeders considered the impurities of their races as of minor importance. They could be gotten rid of by a careful choice of the best and most typical ears, and the saving of seed for sowing had of course to be accompanied always by some such kind of selection. The exclusion of inferior ears was more or less considered as the necessary means of keeping the races true to their standard type. Improved races, as a rule, were more responsive to soil, manure and treatment than the local varieties. It is, however, unavoidable that, with the straw of the manure, some stray grains of these inferior sorts will, from time to time, and not rarely, come onto the fields. Here they will be content with a lesser supply of food, space and care than the improved races, and thereby be enabled to grow faster and multiply more quickly. It is hardly conceivable how soon these inferior races may multiply themselves to such an extent as to occupy large parts of the field, supplanting the ameliorated type and lessening the harvest to a noticeable degree. In bad years, even the wind oats which scatter their small seeds to the winds and thereby yield nothing at all for the harvest, may be seen to replace more than half the stock of the fields

Under such circumstances, keeping the races pure by means of selection is evidently a necessary part of all intelligent culture. It is the first thing to be done, but it is considered hardly worthy the name of improvement. In Ger-

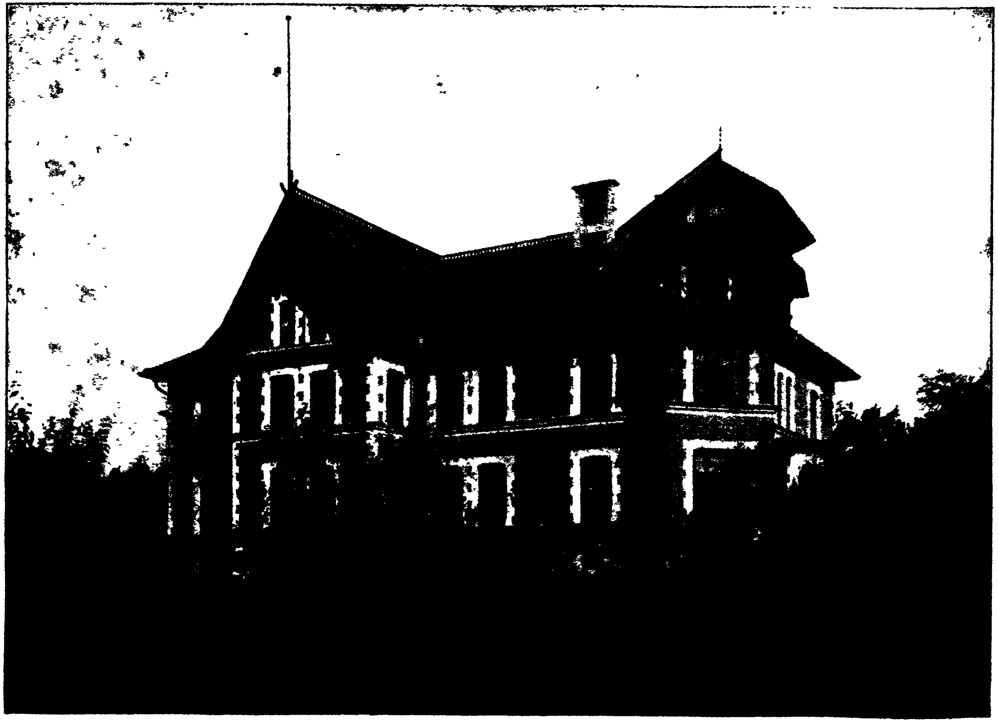


Fig. 17. The Laboratory of the Agricultural Experiment Station at Svalöf, Sweden.

many, real improvement was treated as a separate occupation and was considered as requiring a large amount of study, and the devoting of oneself to a proposed aim. The general custom was to start such experiments from the best local or improved varieties by an initial choice of a certain number of typical heads. Such a group of selected plants was called the élite, and this élite had to be ameliorated according to the prevailing demands or even simply in accordance with some ideal model. Year after year, the best ears of the élite group were chosen for the continuance of the strain or family, and slowly, but gradually, its qualities were seen to improve in the desired direction. After some years, such a family might become decidedly better than the variety from which it had been derived. Then its yearly harvest would be divided into two parts, after having been sufficiently purified by the rejection of accidental ears of minor worth. The best ears were carefully sought out and laid aside for the continuance of the élite strain, but the remainder were sown on a distant field in order to be multiplied as fast as possible. By this means, after a multiplication during two or three generations, its product could be used as seed grain for the farm or sold to others for the same purpose. Each year the élite would, of course, give a new and better harvest which could be multiplied and sold in the same manner.

From this description, it may easily be gathered that an improved variety, produced after these principles, cannot be called a race in the ordinary sense of the word. Only the élite itself is a pure race, but it consists of only a small family, cultivated on a single farm. The extensive cultures of the succeeding years, however, are not related to one another in the ordinary way of ancestors and descendants. They are, or at least they should be, the ends of succeeding side-branches of the élite, each branch being surpassed in excellence by its successor, and therefore no longer deserv-

Fig. 18. The Storage Building of the Agricultural Experiment Station at Svalöf, Sweden.

ing to be kept in culture. Since only the élite can produce the most advanced side-branches, the production of seed grains has always to return to it or rather to be started anew from it. No farmer should sow his own harvest, because if he does so, he will soon be surpassed by others. Or, if he should be able to do it without harm, it can last only for a few years, since he cannot keep up the selection which alone is adequate to maintain the race at its highest standard.

Contrary to the opinion of Hallett, who claimed to produce his ameliorations by giving his plants large space, ample manure and the best possible exposure and treatment, the German principle was to make the selections under precisely the same conditions as those of the ordinary field cultures. It was assumed that changes produced by the outward conditions of life, were only of a temporary and and not of an hereditary nature. Hereditary qualities were assumed to be innate and independent of environmental influences. Only by means of selection could they be fixed, increased or lessened, and finally changed in definite ways. On the ground of these views, selection was the true factor of the improvement, and since the breeder could select according to his own wishes and ideals, it was believed that selection was a means of changing any plant in any direction, and to any desirable degree. By direct changes, brought about by local and individual differences in the life conditions, this selection could only be misled, since such a change might be taken for an hereditary improvement whenever its real cause was hidden. Therefore it was a rule to reject all specimens which could possibly have profited by an exceptional amount of space, manure or light, before beginning the real selection.

Such were the more or less clearly understood, and more or less generally accepted views in central Europe at the time of the establishment of the experiment station at Svalöf. No

reason to doubt their validity was at hand, and moreover, the evidence was only scanty and widely scattered, without affording sufficient material of facts for a thorough criticism. The results of the English breeders were hardly accessible at that time, and so the Svalöf experiments had to begin by following the German principle. Summing up the principal features, we may state that it commenced with the choice of a certain number of ears, and cultivated their progeny as a mixed family, in which, year after year, the best heads were chosen in adequate number for the continuance of the race.

The experiment station at Svalöf has accepted the principle that the selection cultures must be made on the same soil and under the same conditions as the ordinary field cultures. Especially, the distances at which the seeds were sown from each other had to be the same, this being a point which had often been dealt with in another way, since by a somewhat larger relative distance, the treatment and the final distinguishing of the single plants is notably facilitated. This principle has been found to be reliable, and has been kept unchanged through all the periods of experimentation, which have supplanted almost all others.

Moreover, the methods of testing and comparing have been largely improved. Instead of the personal appreciation of the qualities of the ears, accurate measurements have been adopted. An elaborate book-keeping required the statement of a large number of qualities by short indications, and figures came to be preferred to descriptions. The length of the ears was given, their form indicated by width and breadth, and by the place where both reached their maximum value. The density could be measured by the number of nodes and spikelets, and in the latter, the number of single kernels could be noted. Other valuable qualities required separate tools and instruments, and even the degree of brittleness had to be expressed by figures.

By these means it was soon found possible to extend the experiments to a previously unknown number, and, at the same time, to obtain far larger deviations from the initial type in a relatively short succession of generations. Thereby the breeder was enabled to collect his experience on a scale large enough to yield the material for a full experimental criticism of the whole method. The result of this part of the work proved, however, to be not at all satisfying.

Of course, the first selection experiments were conducted according to the local needs of the farmers. Among oats the celebrated races of the Probstei were cultivated, among the peas the variety called Victoria, and among wheat the squarehead sorts. Shortly before, the French breeder, Vilmorin, had produced a new variety of oats to which he had given the name of Ligowo oats. It was tested at Svalöf, and its introduction into Swedish agriculture has been one of the best successes of the young station. In the same way, two of the older varieties of barley, the "Plumage" and the "Prentice," were recommended and soon largely distributed. The testing was always performed under strict comparison with the local varieties, of which, for this reason, a considerable number were kept in culture.

In the meantime, the deficiencies of the method could not escape observation. All those which were of a purely technical nature could be overcome, and on this side of the problem a high degree of perfection was attained. But there were other weak points which were related to the very foundation principles of the method. Among these, the principal one was that the continuous selection of the best specimens in an arbitrary direction did not lead to improvement in all cases. Quite on the contrary, success was rare; so rare, even, that it could almost be looked upon as an exception. The fact itself was not new, since in Germany, also, only

in exceptional cases a real improvement had been obtained. But, of course, usually only successful instances are published, and concerning the remainder ordinarily no evidence is at hand.

In Svalöf, however, where numerous experiments of the same kind, but with different varieties of cereals, were conducted side by side, the fact could not escape observation. Soon, the idea suggested itself that if success is an exception, the principle involved in the method can hardly be a valuable one, at least, not one on which the breeder may confidently rely.

An instance may be given. As such, I choose the Chevalier barley, which is one of the most valuable kinds for the brewers. In Sweden, it has the defect of being often exposed to lodging or lying down. The culms are too weak, and are thrown down by wind and rain shortly before the time of the harvest. Great losses are usually the consequence, and it was considered a distinct necessity to breed a Chevalier barley with culms stiff enough to resist these evils, even on the hard soils of the middle parts of Sweden. Here the culture of this variety had been tried on a large scale, but was given up in consequence of the defect alluded to. In order to introduce it anew, and to restore the brewer's industry to its former degree of development, the Chevalier barley had to be improved and adapted to the circumstances. This demand seemed the more proper, since elsewhere and especially in Germany, this barley had attained the height of its renown exactly at that time. There could not be any doubt that it was the best kind for brewing purposes. On this account, it was cultivated at Svalöf on a large scale, and with all possible care. It was submitted to repeated selection with the distinct purpose of giving it stiffer culms. The results, however, did not correspond with the expectations. The harvest remained comparatively small, and the quality

was not that which might be expected. The cultures were correspondingly increased in extent, and the selection made more intense. The whole experiment was worked up to such a degree of perfection that it could not only be compared with the most renowned German pedigree cultures, but might even be considered as a test by which the value of the principle itself could be judged.

Notwithstanding this, the result was an absolute negative. It was simply impossible to get rid of the propensity to lie down. No real improvement could be reached. After many years of hard work with steadily improved instruments and methods of testing and selection, the experiment had to be given up, since there was no ground for the hope of finally reaching the aim.

At the same time, a considerable number of other selection experiments had been carried on. Some of them gave the desired results, but others did not. The positive instances were only few, and although they have produced quite valuable new races, and have distinctly contributed to the improvement of agriculture in southern Sweden, it was clear that they could not afford sufficient proof for the reliability of the principle.

Success remained an exception, and exceptional improvements were not the aim of the work of the station. Distinct problems it had to solve. It had to free the old varieties from definite defects, which impeded their more extensive use. A method which would give its results in some cases and in others not, could not be considered as involving the principle wanted. On the contrary, the conclusion had to be granted that in the positive cases, the result might be due to quite other causes, and that if it were only possible to discover these, the whole system might be thrown over and replaced by sure and more reliable principles. The German idea that it was in the power of man to improve his

plants in an arbitrarily chosen direction, was manifestly contradicted by nature. The plant develops itself after its own capacity, but does not suffer itself to be forced into other ways.

The principle of slow and gradual amelioration by so-called methodical selection was thereby condemned. The squarehead wheat showed itself to be as little amenable to improvement as the barley. Even the oats could not be improved. The new varieties which were occasionally acquired by the process might as well be considered as accidents. Among them was the Princess barley, which had been derived from the introduced Prentice barley, and which gained a high reputation and extensive distribution. In the same way, the Plumage barley yielded some valuable novelties. There was no reliability in the method, nor could it be discovered why a result might be obtained in some cases, and in others not. It was clear that the solution of the great problem was to be sought in quite another way.

In the next chapter I propose to deal with the further experiments of the station at Svalöf, which led to the discovery of the principle that the elementary species are the true material for selection, and that they are numerous and varied enough to satisfy all the present demands of practice. In order to make this description independent of all discussions of the older principle, I will once more point out the essential differences between the German method and the work of the previous English breeders, as described in the former chapter. In doing so we have to exclude the views of Hallett, who partly participated in the ideas of his countrymen and partly held the same opinion as the Germans. The contrast now assumes this aspect: Improvement may be obtained by selecting single excellent individuals, and experience teaches that they will yield a constant and uniform progeny. This is the old English principle, by means of

which new races are not created but simply isolated from among a mixture. The alternative principle is, that a race may be improved and educated in arbitrarily chosen directions. The original race is thereby assumed to be pure and uniform, and thus there is no reason for beginning with one single individual. It is even better to start from a handful of ears, and to select in each generation a similar number, in order to be sure that all characters which are not consciously considered in the selection may remain in the average condition which they held in the original variety.

Concerning the causes of the improvement in this repeated selection, two contrasting views have been discussed. Hallett assumed that variability was induced or at least increased in the desired direction by his treatment. In Germany the opposite view was held, and it was even assumed that all changes induced by outer influences had no hereditary power at all. They were considered as delusive, and the principle followed was to exclude them carefully. Internal causes were the real source of variability, and these had to be guided by selection. And since those internal causes, from their very nature, were not accessible to man, selection was considered the only real means of improvement. It worked slowly and often did not work at all, but wherever a success was obtained, it was ascribed to the influence of this selection.

As I have already stated, methodical selection was assumed to produce races which could only be kept up to their high standard by a continuation of the selection. This point was of the highest practical interest for the breeder, since it kept the production of the seed-grains of his race in his own hands, at least for a long succession of years, and thereby enabled him to secure very considerable profits. On this account it is only natural that many breeders of cereals of the present time still adhere to these old convictions.

As an instance, I may cite the station for breeding cereals and potatoes at Nassenheide near Stettin in Germany, which is under the direction of Count Arnim Schlagenthin. Although in the main it offers for sale the new races produced at Svalöf by the methods to be described in our next chapter, it recommends the sale of the grains on the basis of the old views of dependency on élite strains instead of simply laying stress upon the purity of its products.

Finally, a question is to be considered which has more of scientific than of practical interest. Though the isolation of individuals of exceptional excellence and the methodical improvement of races are absolutely contrasting principles, it is evident that they do not, in reality, need to exclude one another. Quite on the contrary, it might be conceded that isolation is one process, but that the isolated types themselves can afterwards be improved by selection. This conception would lessen the difference between the opposite views and at the same time make them comply, at least apparently, with the idea of an origin of species in nature by means of slow and gradual changes. Theoretically, no objection could be made to this proposition and it would only remain to test its value by direct experiments. Practically, however, the proposition would be a purely hypothetical one, instead of being derived from the experience of the breeders, and it is manifest that these would thereby as well lose their significance as a support for Wallace's views on the origin of wild species.

C. THE SVALÖF METHOD OF PRODUCING IMPROVED RACES.

The criticism of the reliability of the German method of race-amelioration was part of the work during the first period of the operation of the experiment station at Svalöf. It had not yet been conducted to a definite conclusion, when, in

the year 1890, the present Director, Dr. Hjalmar Nilsson was appointed as such. With a broad conception of the practical interests of Swedish agriculture, he combined the conviction that only really scientific studies are adequate to the solution of difficult practical problems. A thorough knowledge of the laws of variability and inheritance seemed to him to be the principal requirement for the solution of the prevailing problems. As we shall presently see, it has afforded him the answer to the main questions and afterward led him to the establishment of his great principle of correlated variability as one of the principal foundations of agricultural plant-breeding. But the interest of this subject is great enough to justify a separate treatment, and so we shall at present defer it to another occasion.

Before going into details, I will give a short survey of the work, in order to facilitate its appreciation. Progress has chiefly been achieved by the discovery of the numerous elementary units of which the ordinary varieties of cereals are built up. That varieties were, as a rule, neither pure nor uniform, was a fact that could no longer escape observation, and selection as a means of purifying the races and of keeping them up to their main standard had already received general recognition. But no agriculturist had even the remotest idea of the real state of their compound nature, and not even the work of Le Couteur and Shirreff had been sufficient to afford such a conception. A protean group of types was found to constitute each so-called variety. These types were seen to be different from one another in a previously unsuspected degree, covering a range of variability adequate to comply with almost all the needs of practice. Moreover, these types proved to be constant; they had only to be isolated and multiplied to yield new and uniform races, directly suitable for the farmers' purposes.

Confronted with these new facts, the current conception

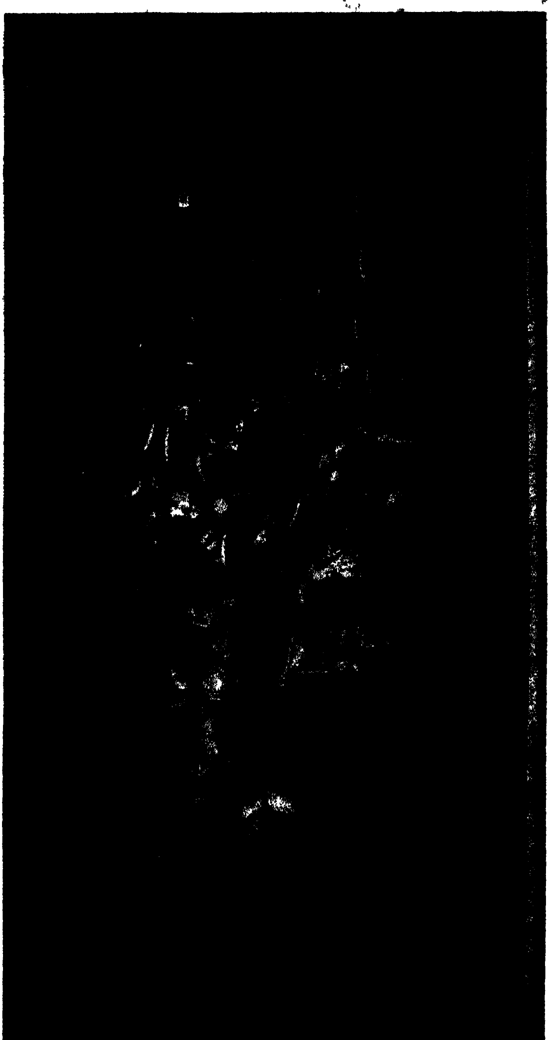


Fig. 19. Svalöf Concordia pea, a most productive erect new variety of green peas, produced at Svalöf.

of variability itself had to be reconsidered. It is rather a state of polymorphy. The idea of continual changes can hardly be connected with it. It is the existence of numerous different forms, each of which is simple and almost invariable. The term should convey the idea of a mixture, but hardly refers to actual changes in the constituent types.

Nilsson began his work by selecting a considerable number of samples from the varieties on the fields of the station, but in doing so, he still followed the prevailing method. Each sample was sown on a separate field plot and progress was tested in regard to purity and quality. Nearly a thousand lots were cultivated, but the result was as unsatisfactory as before. Everywhere the groups were seen to be heterogeneous and to consist of a more or less motley mixture of types. The samples, however, had been chosen under the assumption that they were uniform, and it had been expected that they would yield each a uniform progeny. This however, was not the case, and doubts arose as to the reliability of the whole process of selection. If the progeny does not correspond to the mother plants from which it is derived, how can we tell that the next selection will produce a generation with the desired qualities?

All reliability of the selection-principle seemed to disappear, when, fortunately, an accidental observation was made which at once changed the whole aspect of the question. Some few cultures were discovered among the thousands which bore only one type. They were as uniform as the remainder were heterogeneous. Concerning the initial choice of the samples, an elaborate record had been kept, and this enabled Nilsson to discover the cause of the purity of these exceptional cases. According to the accepted method, each sample had consisted of a certain number of ears, which were as similar to one another as could be expected, and which were therefore, simply taken to belong

to the same type. But, of course, the number of ears had been different in the different groups, some being common and represented by numerous individuals and others being rare. Among the rarest, some types had only been met with in one single head, and since the number of the ears had been entered for each, it could be made out at the time of the testing of the cultures, which among them were in this exceptional condition.

To this accidental circumstance, combined with the exact scientific method of keeping extensive records, the discovery of the cause of the diversity of the cultures was due. For precisely those cultures which were derived from one ear only were found to be pure and uniform, all others offering to the eye a more or less motley assemblage of forms. Hence the conclusion that cultures, in order to be pure, must be started from single ears. Two or more ears may seem similar enough to be considered as representatives of the same type, while in reality they do not afford sufficiently reliable marks.

On the basis of this discovery, a distinction had to be made between the selection of samples and the selection of individual ears or panicles. The older experiments had always been started from multiple samples, according to the prevailing views, and it became at once clear that at least one cause of their usual miscarrying must be sought in this course of procedure. They must be designated as selections of groups or of families, and could even appropriately be denominated selections of crowds, an expression which would at once convey the idea that the terms of selecting simultaneously more than one individual are intrinsically contradictory.

Contrasting with this old principle, the new one was designated as that of the separate selection or separate cultures. It has also received the name of pedigree-cultures,

but with another significance to the word than that used by Hallett, as we shall soon see. It opened the prospect of a new manner of operating and that at a time when the results of the previous methods had become such as to make all further trials almost hopeless.

As yet it was, however, only a presumption, resting on the small evidence quoted. It was more an indication of what could be expected than a proof of what really was. It had first to be tested. This was done at once, and on as large a scale as possible. It was in the summer of 1892 that the described rare uniform plots were seen, and in the harvest of the same year a renewed search for starting-points for new races was made. But this time each ear was kept separate, and two or more heads were combined only when they were gathered on the same individual plant. Some ears were chosen as the best representatives of their varieties, others as deviating from the type in one respect or another. All in all, about two thousand ears and panicles of different species and varieties, representing as many divergent types as possible were selected. The grains of each were sown on a separate plot, and next year all the groups were descended from one single mother plant each.

The results of this trial greatly exceeded all previous expectations. Almost all the numbers were seen to be uniform, all the offspring of a single plant being wholly similar. Exceptions there were, but they were exceedingly rare. For instance, among the 422 cultures of oats, 397 were uniform and only 25 multiple. But of course it could be expected that among so large a number of ears, some hybrids would be met with, and others which would be only partially self-fertilized, but for the remaining part contaminated by the pollen of their neighbors. In either case, the progeny would be dissimilar, and especially in the former the splitting up of the hybrids would give rise to quite a considerable

degree of dissimilarity. The cases of such mixed progeny were rare enough to be considered as the consequence of the selection of such hybrids, and special experiments have since given sufficient proof of the truth of this assertion. Leaving these hybrids aside, the cultures of 1893 advanced the importance of the selection of single individuals as the one reliable source of purity, to the rank of an experimentally established fact.

From this fact it could further be deduced that a repeated selection would be unnecessary. The next generation might be expected to be as pure and as true to the type as the first. Moreover, the uniformity was such as to make another selection simply impossible. All the differences which formerly afforded the material for selection had disappeared from these new strains. They were observed to exist among the separate cultures, and allowed a comparison of these in exactly the same sense as they formerly had made possible a choice in the fields. But within each culture no other differences were seen than those unavoidable degrees in development which result from the differences in location between the central plants and those of the border, or between accidentally crowded or locally favored individuals, and the average of the group.

These observations led to the establishment of the second great principle, that of the sufficiency of the one initial choice. After that, the newly isolated type has only to be multiplied and to be kept free from accidental admixtures. On this point, the Svalöf method agrees with the principles observed by Le Couteur and Shirreff, who, likewise, did not repeat their selection. For the industrial side of the work, this principle has a high value. In the beginning, it was feared that the reduction of the commencement of a race to one single head might protract its multiplication so as to require more generations to reach the quantity necessary for

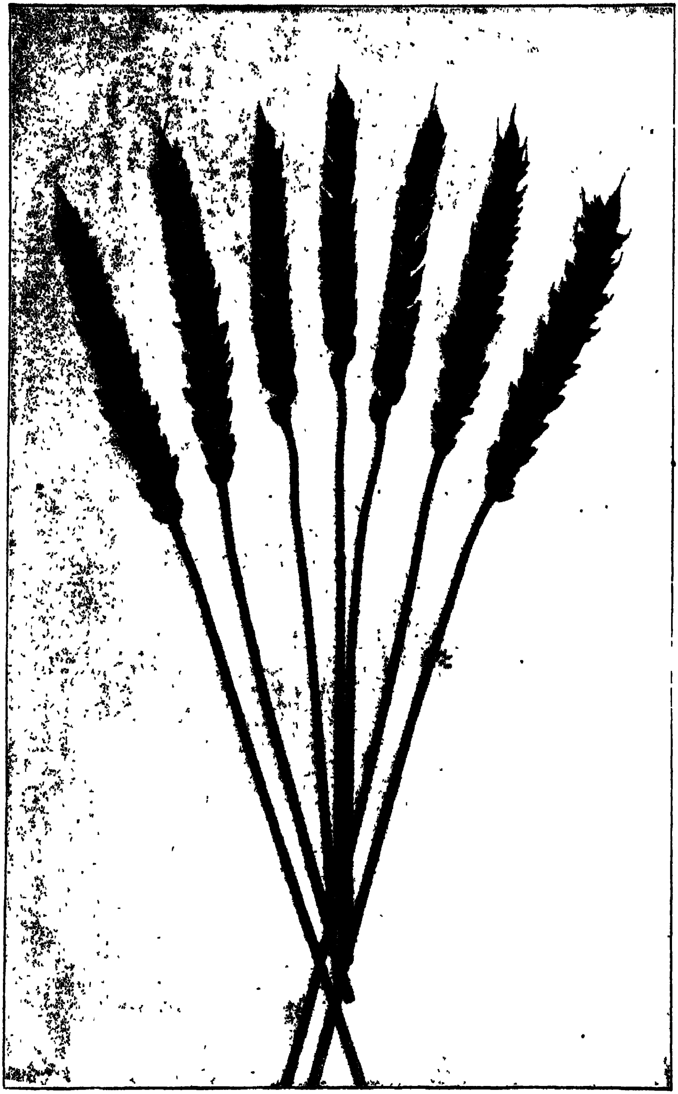


Fig. 20. Svalöf Pearl summer wheat, not layering, early ripening, with full rounded kernels, that keep in the ears at harvest time.

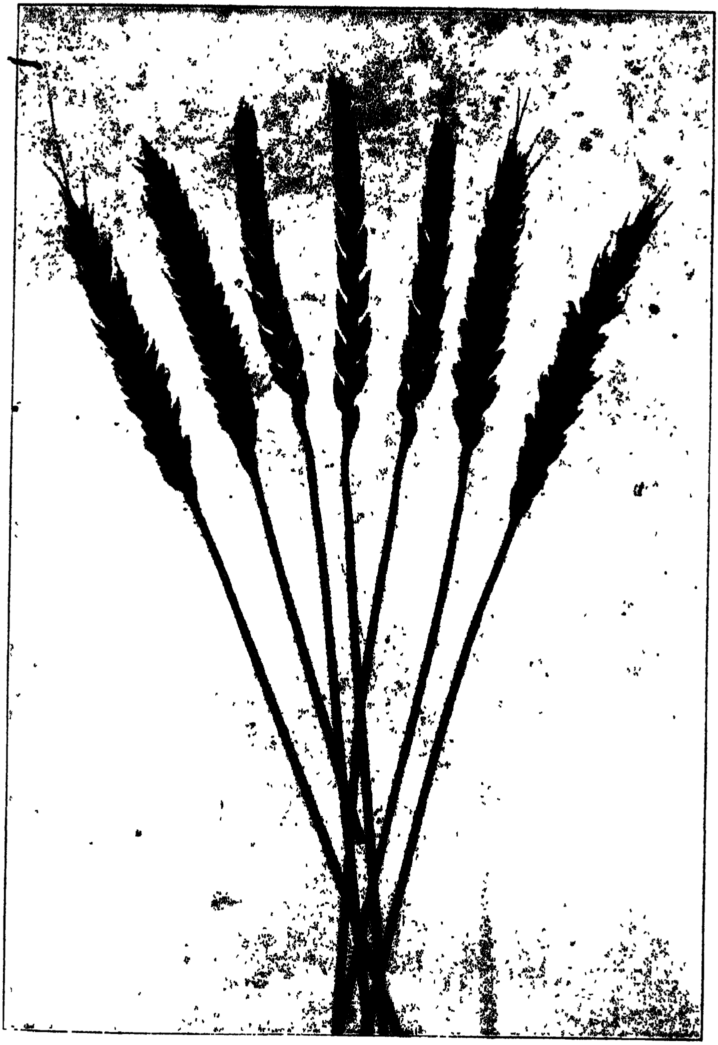
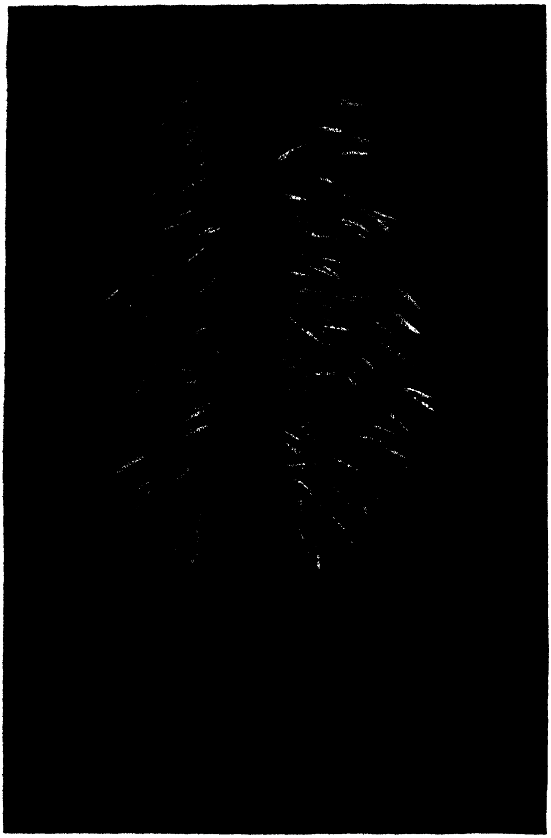


Fig. 21. Ordinary Butt summer wheat, for comparison with the improved variety of the previous figure.

its ultimate distribution. Experience, however, soon showed this fear to be unfounded, since the elimination of all further selection soon overcomes the incipient deficiency. In reality,



Figs. 22–26. Five different types of new varieties of oats, produced at Svalöf.
Fig. 22. Flag-oats.

the multiplication of a separate culture may go on as fast, or even faster, than that of an old-fashioned methodical selection.

In the fall of 1893, these new principles could be consid-

ered as wholly established. At once they were raised to the rank of an exclusive method. Of course, the existing cultures could not easily be given up, but they could be rapidly diminished. After three years, almost all the experiments were of the separate-culture sort, and of older varieties only a small number were kept, and destined to afford the material for a comparison of the novelties with the types they were called upon to replace. Since that time, the selection of crowds, or even of small groups of heads, has completely been abandoned at Svalöf, and all the numerous new sorts which the station has since introduced into the trade are derived each from a single individual. Consequently, they are absolutely pure, and purity is for them such a matter of course that often it is hardly mentioned at all.

Pure races, however, are by no means the sole, or even the first, requisite of the farmer. Above all, they must have better qualities and yield a richer harvest than the ordinary varieties. Thus the question arose whether the separate-cultures would satisfy in this respect. But even here they were found to surpass all expectations. Of course, of two thousand types, all cannot be excellent. But manifestly this is not at all necessary. It is quite sufficient, if among them, some few are found having really excellent qualities. A careful comparison of the families of the year 1893 showed that their mutual differences were much greater than could be surmised from the amount of variability observed in the fields at the time of selection. Moreover, the separate-cultures complied with the most diverse requirements, some being highly resistant to frost, others to diseases, some being suited for hard and others for light soils, some being early and others late in ripening, some surpassing others by the stiffness of their culms, the length of their ears, the number and size of their grains, and so on. Hardly any demand could be pointed out, with which at least

one of the new varieties did not comply. The experimental fields were in some sense large exhibits on which each farmer could seek out the types that would best suit his soil and his local conditions.

This choice, however, had to be made at the station itself. It was impossible to multiply even many hundreds of the new sorts. The best had to be chosen, and in order to do this, all of them had to be compared with the utmost care. A second line of work had to be set up, as important as the first, but requiring a far larger amount of labor. The new varieties had to be studied and tested, and to be tried from all points of view. The study had to embrace their whole lifetime, and the botanical marks and biological symptoms as well as the industrial qualities, and their requirements with respect to treatment. The botanical and biological characters of the new sorts came first, because they were more easily studied and because they afforded an opportunity of reducing the number of the strains considerably without the time-consuming and expensive tests of the industrial qualities. In the meantime, all the families were multiplied as fast as possible. As soon as some fell out, the space left free was occupied by the remaining strains. In this way, nearly the same extent of the field was sufficient for the whole group, during a series of years. In the end, only a few remained, but these had been tested in all directions and found to be the very best. Of course, they had also been compared with the ordinary unselected varieties, and been proven to far surpass these. Five or six years of continuous testing and of corresponding multiplication are usually required before the end is reached. It is quite sufficient when some few new varieties are yearly added to the stock. So in the year 1901, eighteen excellent new types were offered to the trade. Among them, were five new kinds of wheat, six of barley, three of oats and four of

vetches. Each new kind, of course, is given a separate name which partly indicates its quality and partly its origin. As instances I may give the Svalöf Grenadier wheat, the Svalöf Swan-necked barley, the Svalöf Great Mogol black oats and others. From the details given, it may easily be gathered that the multiplication and comparative study of the isolated races embraces the largest part of the work performed at Svalöf. Besides this, the initial choice and the starting of the new varieties is only a matter of temporary concern. The comparative studies require the trials of many hundreds of pedigree-cultures, and accordingly an accurate system of book-keeping is one of the essential features of the work. From its first isolation each culture is designated by a number, which it retains until it is abandoned or until it is judged worthy of introduction into commerce. Then, of course, the number is replaced by an ordinary name, as quoted above. The book numbers at Svalöf consist of four figures, the first of which is a zero, which is prefixed to avoid all confusion with other numbers. The second figure indicates the group and the two remaining ones relate to the special sort. So a dwarf Ligowo oats is called 0313, and another kind of Ligowo oats which was afterward recommended as Svalöf Ligowo, bore the number of 0353.

The amount of this book-keeping is almost incredible. In the year 1900, some 2600 numbers were in culture, partly relating to different grains, including corn, and partly to leguminous plants, such as peas, beans and vetches. To these numbers must be added 138 comparative cultures of races almost ready for introduction into the trade, and among these only twelve older ones were found, the remaining 126 having all been isolated by the new Svalöf method. Further, the book-keeping was increased in the same year by 431 numbers afforded by the progeny of mother plants

which had been selected anew in the fields during the preceding season. The book-keeping embraces the complete botanical description of each new sort, from its germination until the time of the harvest, with all the details required for the controlling of its constancy and uniformity, and for the study of all those qualities upon which the introduction into general agriculture will ultimately depend.

I have purposely left the hybrids out of consideration until this time. In the beginning we saw that, although uniformity is the prevailing rule for the progeny of a single mother plant, exceptions regularly occur. These have been ascribed to the effect of accidental crosses. Until some time ago it was assumed that crosses were of common occurrence only with rye, the other grains fertilizing themselves. But experience has shown that this is only an average rule, and that everywhere in the fields accidental crosses may occur. Their progeny are, of course, hybrids, and these may split in the next generation according to distinct laws, as studied for cereals by Rimpau and other investigators. Any character which was different in the two parents of the cross, may thus split in the progeny of the hybrid, and in this way new combinations of characters may arise. Experience, however, shows that in ordinary fields almost all possible combinations may be met with, and it is to be presumed that at least the greater number of them are due to crosses in previous and, perhaps, in long-forgotten years. In the following generations, these new combinations of character may become fixed in part of the progeny of the hybrids, and it is a well-known fact that such constant races are the ordinary results of natural and artificial crosses. Hence, we may conclude that some, and perhaps many, of the types which may be selected and isolated in the fields and which prove to be constant races must be of hybrid origin.

Whenever such an original hybrid is found in the field

and selected for some peculiar quality, it will repeat the same splittings in its progeny and thus be found not to give rise to a pure and uniform race. This, however, is no drawback. On the contrary, it often affords a means of acquiring new and useful varieties. The selection has only to be repeated, the hybrid group being treated in the same way as the cultures of the original fields. For each type one ear must be selected, and its kernels must be sown separately. According to the ordinary rules of hybrids, some of these separate cultures will at once prove uniform, but others will repeat their splittings. Among these, the choice must be repeated once more, and by continuing this process we may finally succeed in getting all the possible combinations in constant and uniform races. These, though of hybrid origin, have definitely lost the character of variability, which at the beginning distinguished the progeny of the original cross. They are further cultivated and tested in exactly the same way as all other separate cultures, and may yield as valuable agricultural varieties as these.

The work of Svalöf is not connected with the origin of the elementary species which are observed in the field. This is a question of purely scientific interest. Two possibilities offer themselves. Either the high degree of variability is old and the same elementary types which are now existing have already existed for centuries, or the production of new varieties is steadily going on, affording a cause of increasing variability or, at least, of a changing group of units. In the first case the mixtures would be constant and only exposed to accidental losses by the crowding out of some of their rarer constituents. In the latter case, however, the process must be assumed to be a slow one, and the existence of hundreds of types is no proof of a high degree of changeability. This conclusion will easily be arrived at from the following considerations. The ever-occurring crosses must

have the effect of rapidly increasing the number of types, even if ordinary mutability is slow in producing new units. For, by this crossing, each new unit will become united

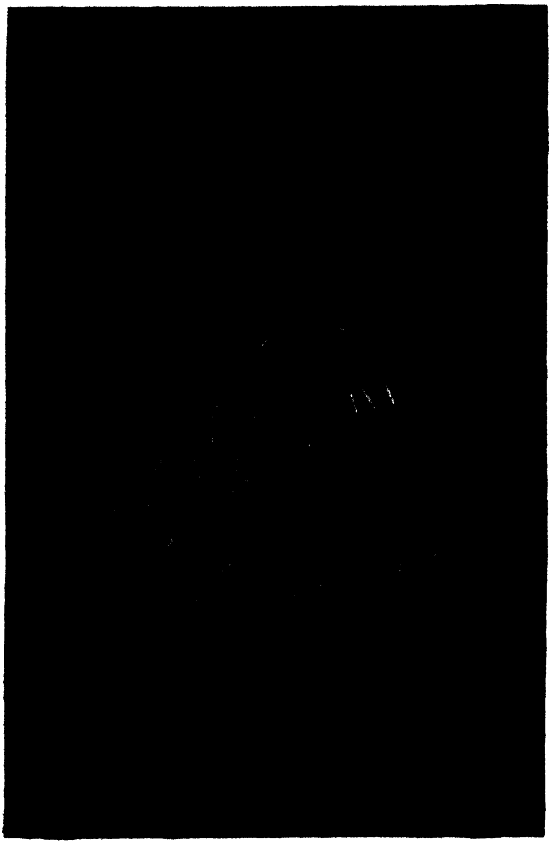


Fig. 23. Stiff-branched Svalöf oats.

with many of the existing types and, in the end, perhaps, with all of them. In this way, the production of one really new unit will tend to double the number of the existing types, and, in the cases of many garden flowers, where such

crosses have been artificially made, the fact that one new character by this means yields a very large number of new varieties is universally known, and one of the most ordin-

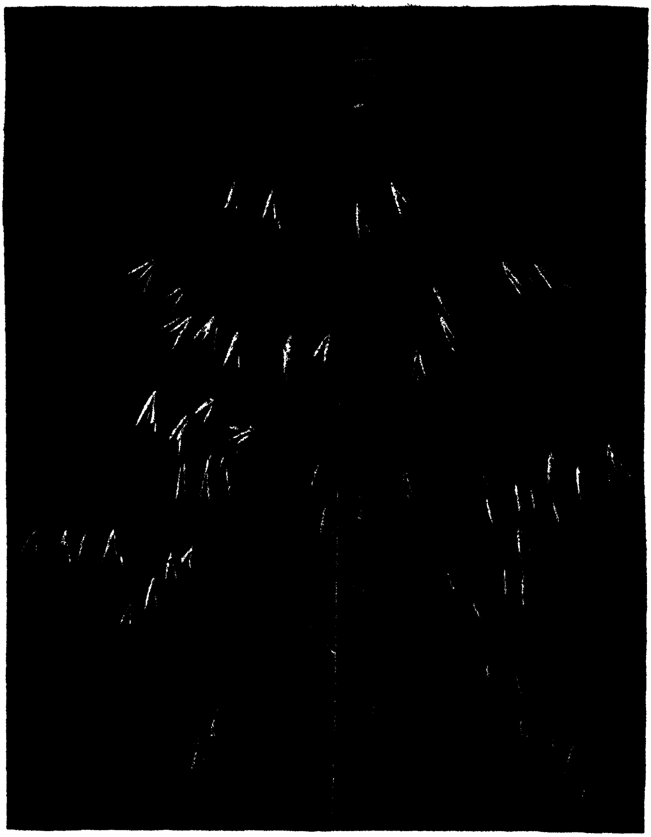


Fig. 24. Svalöf oats with spreading branches.

ary means of producing novelties. Moreover, if one new unit may double the number of the separate types, a second new unit may tend to increase it fourfold, a third eightfold, and so on. From this calculation it may be seen that even

a thousand separate types of combinations do not require more than ten mutually independent changes. Or, in other words, the wide range or variability observed in grain fields may be the effect of the production of a few novelties, combined with a sufficient degree of intercrossing. Hence, it follows that one real change of some character in a year, or even in ten or more years, must be considered as wholly sufficient for an explanation of the observed variability. If we take it that these changes appear suddenly, or in other words, are mutations, then an ordinary degree of mutability, such as is quite common with horticultural plants, seems to be all that is required to explain the numerous types observed at Svalöf. The main difference would be that in horticulture all profitable varieties have been observed and isolated as soon as they have appeared, but that in agriculture they have been allowed to pass without observation, or at least, without appreciation. Consequently, the larger horticultural groups, such as asters, carnations and dahlias, now contain hundreds of well-defined, pure and uniform varieties, but the agricultural varieties are still almost everywhere mixtures awaiting the process of sifting and testing.

The experiments of Svalöf, however, give at least some evidence concerning the probable origin of the variability of the cereals. Up to this time I have described the pedigree-cultures as constant and uniform, and only excluded the case of the hybrids. But even within the purest races deviations may occur from time to time, though rarely, and these may be compared with what probably happens in the field. When a race is started from one selected mother plant and multiplied during some years so as to cover hundreds of acres, it is ordinarily seen to keep wholly pure, all the thousands of individuals displaying the same characters and qualities. This is precisely the special feature and the advantage of the cultures after the Svalöf principle. But, from time to time, one

single specimen among the hundreds of thousands will sport, deviating in some mark from the main type. As soon as such an event is noticed, the sporting individual is usually isolated and its grains are saved separately.

This is practically nothing more than a new initial selection, a starting-point for a new race, which has to be isolated, multiplied and tested in the same way as all the others, and has at least an equal chance with them of yielding a valuable contribution to agricultural practice. Some very good novelties have been obtained in this way at Svalöf. These changes come on unexpectedly and all of a sudden, exactly as ordinary mutations. No visible preparations and no groups of intermediate forms accompany them. They are at once quite distinct from the main type. But, like mutations, they may be confused with the effects of accidental crosses, and such, though very rare, are also seen to occur in the experimental fields of pedigree-races at Svalöf. Crosses may yield hybrids which will split in succeeding generations as we have seen, and whenever the result of the isolation and separate multiplication of a sporting individual is a heterogeneous group, it must be assumed that the deviation was due to a cross.

On the other hand, such a cross does not necessarily exclude a real mutation, since mutations are believed to occur in the production of sexual cells and so may be limited either to the pollen or to the ovaries of a mutating plant. But this theoretical side of the question does not, strictly speaking, belong to our present discussion, and so it may be considered sufficient to have indicated it. My only aim was to point out the difficulties which here, as everywhere, are found in the way of distinguishing between mutants and accidental hybrids. This, however, has reference only to the special cases, but from a broad point of view the experimenters of the staff of Svalöf are satisfied that real mutations as well as

accidental crosses are occurring in their pure pedigree-cultures, from time to time.

Some instances may be given. Among the cultures of

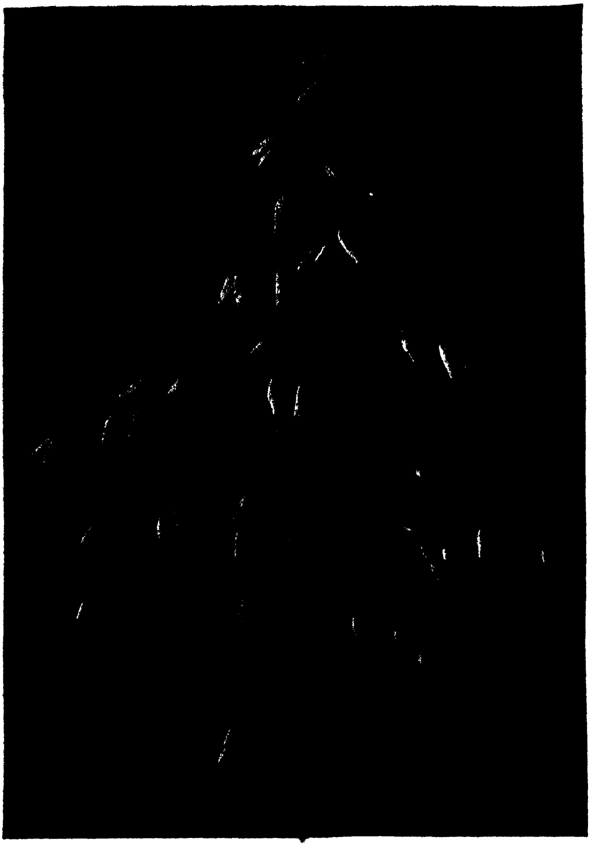


Fig. 25. Svalöf oats with bending branches.

pedigree wheat started from an initial selection made in the year 1892, a race indicated by the book number 0608 distinguished itself by long and stiff culms, combined with an unusually good quality of the grains. But it had two notable

defects, hairy scales and long awns. On account of these deficiencies, it was considered improbable that it could ever be introduced into practice. During four years the race kept

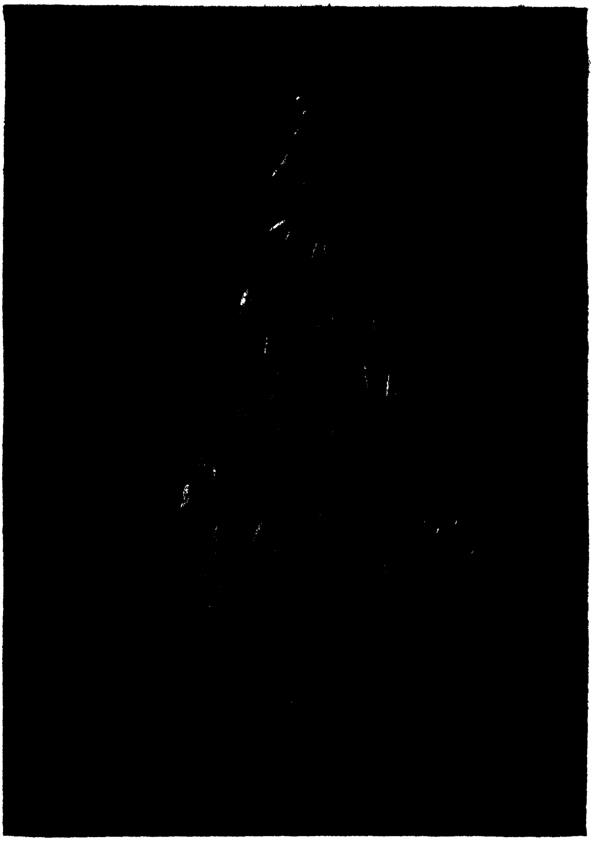


Fig. 26. Svalöf oats with weak branches.

pure and true to its characters, but in the year 1896 one single plant distinguished itself by the lack of awns and by a somewhat deviating size and shape of the ears. Its grains were saved separately and produced a very heterogeneous mixture

of types, among which some showed a new quality in that their scales were smooth. Smooth and hairy scales occurred both on ears with and without awns, thus constituting four principal types in which the remaining differentiating marks gave races of an inferior rank. The next generation still showed some splitting but soon the isolated types became constant and uniform, eight of them being distinct enough to justify a more comprehensive testing. Those which lacked the hairiness and the awns were, of course, considered as distinct improvements, and as such received new numbers in the pedigree-book. Besides these two qualities, they also had denser ears of better construction and stiffer culms, while in other respects they had kept the excellent characters of the parent form. Soon afterward the cold winter of 1900-01 showed them to possess an exceptional degree of resistance to frost, and thereby elevated them to the first rank among all the novelties of winter wheats. In concluding the description of this most interesting case of variation it remains to be stated that the parent-strain from which it sprang has since remained as pure as before, never repeating the novelty nor producing any other.

As a second instance, a winter variety of wheat may be chosen, which had been isolated in 1892 from the Herrenhoff-wheat and bore the number 0516. It is distinguished by long and narrow, smooth ears. It has an excellent quality of grain but weak culms, and moreover, is deficient in its degree of resistance to cold. It was absolutely pure and uniform, but produced in the summer of 1897 one single individual with stiff culms and short and rounded ears. The progeny of this mutant at once proved constant and uniform and quite distinct from all existing varieties, excelling in the marks of its original parent as well as by virtue of a high degree of resistance to cold. It has since remained absolutely pure and constant, has been multiplied during five years and given

to the trade under the name of Zapfenweizen or egg-wheat, alluding to the curious egg-shape of its heads. The parent form which produced this mutation sported twice afterward, but in both cases its products were multiple in the beginning and could be brought to uniformity only after some splittings.

Besides wheat, the cultures of oats, peas and vetches are seen to produce sports, from time to time, at Svalöf. Here, also, the sports are sudden and without preparation or intermediates, each of them at once constituting a new type which is as distinct from its allies as any new form found in the fields. Not rarely these changes are found to relate to the very marks on account of which the parent strain had originally been selected, thus constituting a distinct progression of mutability in a previously determined direction. Among oats one of the most prominent novelties of Svalöf has originated as a mutation in a pedigree-culture which had remained quite uniform during the 8 or 10 preceding years. It is one of the best black kinds and has, curiously enough, been produced by a white variety.

In contrast with wheat and oats, the barley has, until now, remained devoid of novelties. This fact is very important from a theoretical point of view. For accidental crosses may be produced as easily in barley as in wheat and oats. Direct extensive experiments, made at Svalöf, have established this fact beyond all doubt. Hence we may conclude that on the experimental fields, with their pure pedigree-cultures, accidental crosses must be extraordinarily rare, even when compared with the rare occurrences in ordinary fields. Evidently the conclusion must hold good for wheat and oats as well as for barley, and it speaks for the recognition of their sports as mutations rather than as crosses. In other words, it seems probable that wheat and oats are still in a mutative period, like so many of our garden plants, but that barley is

now in a period of stability, as is the case with the larger number of our wild species.

Summing up the main features of this short description of the method of selection developed by Nilsson and his staff at the Swedish agricultural experiment station, we may point out the following propositions: Ordinary varieties of cereals are built up of hundreds of elementary forms which, with few exceptions, have hitherto escaped observation. They may be distinguished in the fields by distinct marks derived from their botanical characters, and will afterward prove to possess corresponding differences in their industrial qualities. They have to be selected but once and afterward will be quite uniform and constant, with the exception of accidental hybrids which, however, will also yield constant and pure races after repeated selection. The purity of the races is such as to be practically absolute, but this does not exclude the occurrence of stray mutations by which new and valuable improvements may be secured. The high variability which is commonly attributed to our ordinary varieties of cereals consists only in the differences among these constituents of the mixtures. But these differences have been found to be so great as to afford material for all desirable selections and to yield new races for all the climates and soils of Sweden, for all the divergent needs and demands of its various industries and even, to a large extent, for exportation into other countries.

D. A CRITICISM OF THE PRINCIPLE OF CONTINUOUS SELECTION.

In the biological sciences the name of Darwin is chiefly attached to two great principles, the theory of descent and the hypothesis of natural selection.

The theory of descent was founded by Lamarck, but it owes its present form to the work of Darwin. By means of immeasurable groups of facts, brought together from the

various results of systematic research and of morphology, of geography and paleontology, he not only contrived to convince the biologists of his time, but also brought the principle of evolution to almost universal acceptance. Especially convincing were his proofs of the numerous adaptations of living organisms to their environments.

The principle of natural selection was discovered by Darwin himself. In a general way he showed that many times more individuals are born than can possibly survive. This results in a struggle for life, in which, apart from casualties, those survive which are the best fitted for their special life-conditions. By this struggle the weak are crowded out, and only the best-fitted become the parents of the subsequent generation. This struggle may be seen at work at every moment and on every field. The elimination of the weaker types by stronger ones also has often been observed. But this is nearly always where different species were competing with one another. Concerning the effects of the intraspecific struggle hardly any observed facts are available. Whether it takes an active part in the production of new species, and in what manner it may be able to do so, is a question far beyond our present observation.

For this reason Darwin relied for a large part on the methods of selection which at his time were in use both in agriculture and in horticulture. He tried to show that the evolution of species at large has followed the same laws that underlie the evolution of races and varieties in culture. In a general way he has succeeded in convincing his contemporaries of the validity of this analogy. Agricultural and horticultural experience, however, were at that time only imperfectly developed, and the improvement of races, though successful in a large number of cases, had no really scientific foundation. It did not afford all the evidence required by Darwin for a thoroughly reliable theory. Complying with

the prevailing belief of the most renowned agriculturists, who considered the breeding of races as a slow process of gradual improvement, he proposed the same slow and almost imperceptible changes as the source of evolution in nature. Since his time experience and theory have made very manifest progress. Especially the principle of the unit-characters, which is the foundation of the theory of the origin of species by mutation, leads us to the acceptance of saltatory changes or so-called sports as most probably Nature's way of producing new forms.

According to this theory species are not changed into one another, but new forms arise laterally from the old stems. The whole strain continues unchanged and only produces from time to time single aberrant individuals. These are the real sources of all progress, and experience has shown, that in the main their new characters are hereditary, and that their progeny remains true to their new types even from its first appearance.

On another occasion I have tried to show that in horticulture experience complies almost wholly with this conception, and the historical researches of Korschinsky give proof of the accuracy of this conclusion. In agricultural breeding-practice the production of new races is a more intricate problem. In many cases their relation to the theoretical conceptions is quite clear, in others it is still surrounded with doubt. In my book on the Mutation theory I have explained how the obvious facts agree with the idea, but it was at that moment impossible to remove all doubts, and so I proposed to return to these questions another time. (Mut. Th. I, p. 82.) Five years have since elapsed and new discoveries have been published which enable us to give a far more complete analysis of the agricultural breeding processes. Especially at the Agricultural Experiment Station in Southern Sweden quite unsuspected facts relating to the variability of

agricultural crops have been discovered as we have seen in our preceding chapters. They are of a nature to turn over all the old ideas concerning race-amelioration and give proof that the methods now generally in use in Europe are faulty from a practical as well as from a scientific point of view. The main discovery is that most of our ordinary agricultural crops are composed not only of elementary species, as was long known before, but that each cultural variety contains hundreds of sharply definite types. These are widely distinct from one another in botanical characters as well as in those properties, which determine their utility from the breeder's point of view, and thus they afford a rich material for selection.

For this chapter I have chosen an application of these discoveries of Nilsson to a criticism of the current views concerning the bearing of agricultural breeding processes on the theory of evolution. Formerly I urged my readers to be careful not to trust too much to these processes and to make use, in scientific discussions, of the most simple and clear cases only (Mut. Theory I, p. 59). The new facts now at hand go to prove that the apparently simple methods of selection have been far more complicated than their authors suspected. The slow and gradual working up of a cereal to a previously fixed ideal seemed to be a process of the simplest possible nature. In reality, however, it is composed of a series of factors which the breeders themselves have not recognized, and which therefore it is now often impossible to discern in their descriptions. In general such an analysis has been made practicable by Nilsson's discoveries. Unfortunately it leads to a less high appreciation of the merits of the breeders (Mut. Th., p. 82), but on the other hand it gives a stronger support to the theory of the saltatory origin of species.

Among the results of the breeders' activity, two main

types of races must be distinguished. In the first place, those races which never become independent of continued selection, and for which the seed must be produced anew in each generation from a stock of so-called élite plants. The other type embraces those varieties which after a shorter or longer period of selection become self-dependent and may henceforth be multiplied without special care.

The prototype of the first kind is given by the sugar-beets. Here the selection works with the ordinary characters of the plant, the amount of sugar, the shape of the roots, the properties of the foliage, and other features. No chance, no sport has produced them, they are simply taken as the plants are offering them everywhere. In consequence, they remain dependent on selection, and though a multiplication during one generation without renewed polarization is often unavoidable, an intervention of two generations is but seldom allowed, and the lack of selection in more than two generations would annihilate nearly all the effect of the whole method. This type of selection is wholly intra-specific and has no analogy whatever with the origin of species in nature.

The other type results in varieties which are as constant and independent as the best horticultural sorts. In some cases they are known to originate in the same way, by accidental sports, as in the instance of Beseler's oats, losing their needles. Here their compliance with the principle of mutation is obvious. In the large majority of cases however, including the most widely known improvements of cereals and other crops, they are said to have been produced by the common, slow, and gradual process of selection. All such cases are surrounded with doubt in regard to their real origin, as well as concerning the degree of self-dependency which is reached at the end. Often practical reasons lead to the preferment of the original seed to one's own

harvest, especially when it is difficult to keep the cultures clean from vicinistic impurities. A race which is really self-dependent may in this way seem to be permanently related to the continuous selection of its pedigree. Such races have been produced at various times by Heine in Germany for rye and wheat, by Drechsler in Göttingen for rye, by Mokry in Hungary for wheat, and in many other instances. It is especially in Germany that this method of slow improvement is adhered to and has given admirable results. One of the best known instances, and for which the historical records are the most complete, is the famous rye of Schlanstedt, produced by Rimpau, which is now largely cultivated all over the central part of Germany and the northern districts of France. In the year 1876 I had the privilege of visiting Mr. Rimpau on his farm at Schlanstedt and of studying his cultures. The élite of his new rye was standing on a small parcel out in the fields, but surrounded by cultures of vegetables and other plants not belonging to the cereals. These minor cultures occupied a large square, which in its turn was surrounded by a complete range of shrubs. Thus, the rye, standing in midst of the square, was sufficiently removed from the neighboring fields to insure it against possible contamination by pollen of other varieties. On the other hand, it was given the same soil and exposure and almost the same cultural treatment as the average cultures.

This race had been started by Rimpau nine years before, in the year 1867. At the time of the harvest of that year he inspected, as he told me, a large number of his rye fields and selected all the ears which seemed to him to noticeably surpass the others. He brought home a handful of them, repeated the trial, and mixed their seeds. This mixed condition in the beginning of his race has now become the weak point, where the whole principle of his method is open to criticism, as we shall soon see.

The seeds were sown the next year, and in the harvest the same selection of the best ears was repeated. Care was taken to exclude all those which, because of some external condition, would have been benefited by more space or more manure than the rest, and would have grown larger by such accidental means. No care, however, was taken to isolate the individuals and to sow their seeds separately, the principle being that all the plants belonged to one race, and that this race had to be improved. This principle of ameliorating a race without isolating its possible constituents seemed at that period to be the right one, though now it can scarcely be considered as scientifically correct.

Each year, in the same way, the best ears were chosen for the continuance of the élite strain, and after the exclusion of all ears of minor value the remainder were sown on a field and multiplied without further selection in order to produce all the seed required for the sowing of the whole farm. It took three or four years to reach this quantity. After twenty years of continued selection this élite strain was so much improved as to produce a race distinctly richer than the ordinary varieties of rye in Middle Germany, and slowly but gradually it found its way, first into the surrounding farms, and afterward over large parts of the country. During this period Rimpau was thereby enabled to sell all his harvest as seed-grain, obtaining in this way a most satisfactory recompense for his labors. Shortly afterward the rye of Schlanstedt was introduced into France, where it soon overthrew the local varieties, especially in the departments north of Paris. Even there it is ordinarily cultivated from original seed, produced directly by Rimpau or multiplied only during some few generations by seed-merchants.

For purpose of criticism it is highly interesting to note how a French agriculturist, Professor Schribaux of the

Fig. 27. A. Rye of Schlanstedt, produced by Wilhelm Rimpau, by slow repeated selection. B. Ordinary rye.

Institut Agronomique of Paris explains the conditions of keeping the Schlanstedt rye up to its original qualities. He says: "In order to do this, care must be taken to sow the seeds on a field which is as far removed as possible from all other cultures of rye. Moreover, the field should be large and protected all around by a hedge of trees and shrubs. Without this precaution the rye of Schlanstedt would soon degenerate through accidental crosses with the local varieties." Such crosses would under any other conditions be unavoidable and soon wholly deteriorate the race (Almanach du Cultivateur 1892, p. 69).

From this judgment, given by an authority who has so greatly contributed to the wealth of northern France by the introduction of this variety, we may deduce some conclusions as to the constancy of Rimpau's rye. It is clear that Schribaux takes the race to be substantially constant and explains the necessity of continued selection only by the impending danger of crosses with varieties of minor value. Hence it follows that the main significance of the pedigree-culture on the farm of Rimpau must be the same, and that at least in later years his pedigree must have gained a degree of uniformity, which was in no need of any further improvements. The real act of effective selection is thereby brought back to the first years, but how many generations of true selection it has taken to render the rye of Schlanstedt uniform and pure, it will of course always remain impossible to tell. The explanation of Rimpau's success must therefore remain largely hypothetical. If now we try to give such an explanation on the ground of the theory of mutation and of the already quoted discoveries of Nilsson we may suggest the following: At the period when Rimpau started his pedigree, his rye fields must have contained numerous elementary species, not observed or distinguished by him or by any other agriculturist of his time. Among the ears

which he selected a goodly number of these aberrant types must of course have been represented, since he selected only those which caught his eye by some striking and useful difference from the main type. Of course, he sought for ears of one and the same ideal type, having a large number of big kernels. But notwithstanding this, his handful of ears must have belonged to more than one elementary species, the real value of which could be judged only in their progeny. Among these units of his selection some must have been better yielders than others and the subsequent selection of his twenty years of pedigree-culture must slowly but surely have eliminated the units of minor worth. This would result in the end in a complete isolation of the best one of all the types, which he originally but unconsciously selected and mixed.

Or in other words, Rimpau's pedigree culture was started as a mixture of a number of excellent types, and his yearly selection has gradually reduced this number, until he had isolated and purified the very best one among them. This point was, of course, only unconsciously reached, but then it must have made his rye independent of all further real selection, reducing the process to the care of excluding vicinism.

If this explanation of Rimpau's process is true, it of course holds good for all similar cases of slow and gradual improvement of agricultural plants by selection. Thereby it would deprive the theory of the origin of species by slight and continuous changes of its last support in the realm of the vegetable kingdom.

It remains to be shown that the new facts give sufficient proof of the accuracy of this suggestion. These facts may be grouped under three heads. First, the general occurrence of elementary species and their constancy. Secondly, a comparison of the value of fluctuating variability and

mutability among cereals, and in the third place, the researches of Nilsson, which have given the leading principle for my suggestion.

Our first point is now becoming generally recognized. The researches of Jordan and of Wittrock show the existence of races for the species of the genus Viola. Other notable instances are those of Draba verna, of Capsella Heegeri, of the Xanthium Wootoni, a variety with half the original number of spines on its burs, and many others.

For myself, I have had opportunities to test the constancy of such elementary forms and in some instances even at the period of their very first discovery. Two local evening-primroses, up to the present time occurring only on a field near Hilversum, where they are growing among the common Œnothera Lamarckiana, have given proof of their absolute constancy in my cultures. They are the O. lævifolia and O. brevistylis, both of which are still seen to thrive on their small native locality. Other instances are the cruciate form of the ordinary European primrose, Œnothera biennis and an analogous variety of the willow-herb, Epilobium hirsutum. Many other instances could easily be added. The conclusion seems warranted that elementary forms may be found in nearly all systematic species, and are as constant as the latter have always been supposed to be. These facts give a strong presumption that the same rule may hold good for the rye-cultures of Rimpau.

My second point relates to the question of the part which fluctuating variability and mutability may have played in the selection-culture of Rimpau. An exact notion of the first phenomenon, as stated by the works of Quetelet (1870) and Galton (1889) found its way into botanical investigations about the year 1894, or nearly twenty-five years after Rimpau started his pedigree of rye. In his time, therefore, no distinction of this kind could be made, and it is only

natural that he took his selected specimens to be the extremes of ordinary variability (1867).

This point of view, and this lack of distinction between the now so clearly contrasted processes has prevailed for a long time among agriculturists. As an instance I may quote the work of Willet M. Hays, now in Washington, which, though younger than the researches at Svalöf, has been conducted independently (1899 Bull. No. 62., Agric. Exp. Station, Minnesota). He has improved the wheat of Minnesota by breeding from the local Fife and Blue Stem races, some better and more yielding varieties, which have now largely supplanted the old types. Besides his practical results, he has given some theoretical discussions, in which he assumes a relation of his chosen mother plants to the fluctuating variability and considers them extremes in the curves which constitute the law of Quetelet. "In each one thousand plants of wheat," he says, "there are a few phenomenal yielders, and the method of single-seed planting makes it practicable to secure these exceptional plants, and from these new varieties can be made" (p. 429). But according to our present knowledge, the isolation of such plants, if they were truly extremes of fluctuating variability, would lead to a regression to mediocrity, as it has been called by Galton, and not to constancy nor to an exact keeping up of the extreme type. Therefore the supposition is allowed that the phenomenal yielders of Hays were in reality representatives of distinct elementary species, which had been hidden until his time. His method of selecting enabled him to single them out, and his new principle of single-seed planting, which led him to his high achievements, at the same time pointed out the way for an explanation on the basis of our present views concerning the different types of variability.

It would take me too long to describe the methods and

cultures of the Minnesota Experiment Station, and I may assume that their leading principles and practical results are well known. But I wish to point out, that exactly in the principle of sowing the seeds of individual selected plants separately, Hays gained a distinct advantage over the slow process of Rimpau and the other German breeders. He found, by his method, that the isolated strains are at once constant and pure. They had only to be multiplied in order to give a new race. Of course, the different mother plants had to be compared in their progeny, and among a large number of such new pedigree-races only one or two were found to be of the very best. The remainder had to be rejected, and only those few most excellent ones could be introduced with advantage into the field-cultures of the state.

If now we compare this principle of Hays with the method of Rimpau we find that the American breeder by one single choice isolated the very best strains and observed them to be constant and pure. The German breeder, on the other hand, by selecting a number of ears, must have gotten an impure race, and needed a long succession of years and a constantly repeated selection to attain, in the end, the same result.

Hence we may presume that if Rimpau, in starting his experiments, forty years ago, had had at his disposal our present knowledge of variability, he would have sown the kernels of his selected ears separately and selected at once among the resulting strains the very one which now bears the name of his farm. No continuous culture and repeated selection would have been needed, and the seemingly slow and gradual improvement of a race by selection would have been avoided.

The proof of this assertion can be given, as has been said in the beginning, by means of the magnificent experi-

Fig. 28. Determination of centgener power of the progeny of individual wheat plants at the Agricultural Experiment Station of Minnesota, at St. Anthony Park. The progeny of each parent plant packed in a sack for separate harvesting. The director, Mr. Hays, in the first carriage. Aug., 1904.

ments of Nilsson at the Swedish Agricultural Experiment Station at Svalöf. Though working only in the interest of the practical breeder, he applied to his selection thoroughly scientific methods and has arrived at the clear and unexpected conceptions of the variability of cereals and other large agricultural crops, which we have exposed in our previous chapters. Summing up their contents in a few sentences, I have first to recall the practical results and the numerous new and productive races, which have been originated at Svalöf and are now rapidly finding approval with the agriculturists of Sweden, and even of Germany and other countries. For scientific purposes they give proof of the validity of the methods employed at that station, and of the accurate nature of the principles involved therein.

Nilsson at first tried the usual German method, but soon found that it yielded its results only in exceptional cases and could not be applied to all the needs of the agriculturists (1885–1891). He then changed his principle and sowed the kernels of numerous selected ears separately or in small groups (1891–1892). The result was thoroughly decisive, for all the parcels grown from mixed seeds gave a mixed progeny, and only those which were derived from one single ear each gave a pure and uniform culture. This unexpected phenomenon was at once made the basis for further experiments and in numerous sowings, where each was derived from one single plant, the strains were almost always found pure and constant. The only exceptions were those in which a hybrid ear had been accidentally chosen. Here of course the ordinary splittings of hybrid progeny were observed, but in choosing among their products, constancy could be reached in many instances.

Therefore Nilsson's principle for all breeding purposes is now to derive his strains from single mother plants. Only such strains give pure breeds. A second discovery made

at Svalöf, and equally valuable for practice and for science, was that of the almost astonishing richness in elementary species among our agricultural crops. Every cultivated species seems to embrace something like a hundred of them, and the cereals were found to include even several hundreds in each of the older species. Moreover the differences between these elementary forms are so great that they cover nearly the whole field of the wants of the practical agriculturist, or, in other words, by carefully searching the field, in almost every case a plant may be found which complies with the ideal sought for. From such a plant a pure and constant race may be derived without other means than that of isolating and multiplying its progeny. No special culture and no repeated selection is needed, the only care being to protect the race against vicinism. On the basis of these facts Nilsson has founded an elaborate method of selecting original plants for his pedigree-cultures and of comparing their value for practical purposes. But though this process is now the prominent part of his work, it has no direct bearing upon the signification of the methods of Rimpau and other German breeders, and so we may leave it here out of consideration.

Our explanation of Rimpau's method now loses its hypothetical aspect. For since it is proven that the ordinary rye-fields contain hundreds of elementary species, and among them many of superior quality, it is clear that Rimpau must have had an assemblage of such types in his original handful of selected ears. To him they may have seemed alike, but they must have been in reality of very different value.

His slow process of selecting must have singled out in the long run, the very best one from among them. Once isolated, this type yielded a constant race, which became independent of all further selection.

The German breeding process has always been one of the

most important arguments for the prevailing selection-theory and was of late considered its last botanical support. By means of the discoveries of Hays and of Nilsson this support has now been broken down, and the victory of the theory of a saltatory origin of species can no longer be doubted.

III

ON CORN BREEDING

In Europe the smaller cereals constitute the prevailing crops, but in the United States of America, corn is king, as the phrase goes.

Yearly about 2500 million bushels of Indian corn, with a value of $1,000,000,000, are produced in this country, constituting almost eighty per cent of the world's total crop. Of this more than 1500 million bushels are fed to cattle and other meat-producing animals, the remainder being partly exported and partly used for different industrial purposes. The total number of beef cattle in the United States was officially estimated in 1904 at 43,500,000, with a total value of $660,000,000.

Over a hundred different commercial products and about fifty kinds of food are derived from corn and its various constituents, the glucose factories alone consuming over 50,000,000 bushels of corn.

There can be no doubt that corn is the most valuable crop in the United States. Cotton, of course, bears the palm as a money crop, but corn is the main supply of food, directly as well as under the form of meat. No single cereal is of the same high importance, and the agriculture of the principal states of the Middle West is almost wholly dependent upon the raising of corn.

Illinois stands first, but Iowa, Missouri, Kansas, Nebraska, and some others deserve as well their name of the corn states. In Indiana the average crop is 33 bushels per acre, a bushel containing in round numbers 100 ears and commonly shelling out 56 pounds.

On account of this pre-eminent importance, all questions concerning the possible means of increasing the crop of corn

are manifestly of the highest value. Our discussion of the different methods of improving cereals has for this reason to be completed by an inquiry in how far and on what points the principles discovered and elaborated in Europe can advantageously be considered in the selection of this dominant American crop.

In the corn states the production of corn has for some years attained its highest degree of development, as far as its acreage is concerned. Almost all the land suitable for corn growing has been given to this crop. Locally, some increase of the area may still be possible, but it is of no real importance for the total amount of the crop.

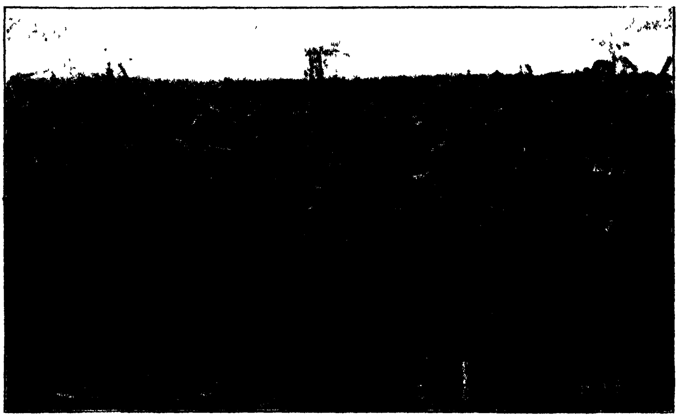


Fig. 29. Breeding block of corn which has been bred for high oil content on the farms of Funk Bros. Seed Co., Bloomington, Ill.

Hence, it follows that an increase of the harvest can be obtained only by an augmentation of the yield per acre, and since the demand for corn is incessantly increasing and the prices are becoming correspondingly higher, the question how to increase this yield has become a most urgent one. The land values are constantly rising, and handsome profits are possible, but to secure them better methods must be employed.

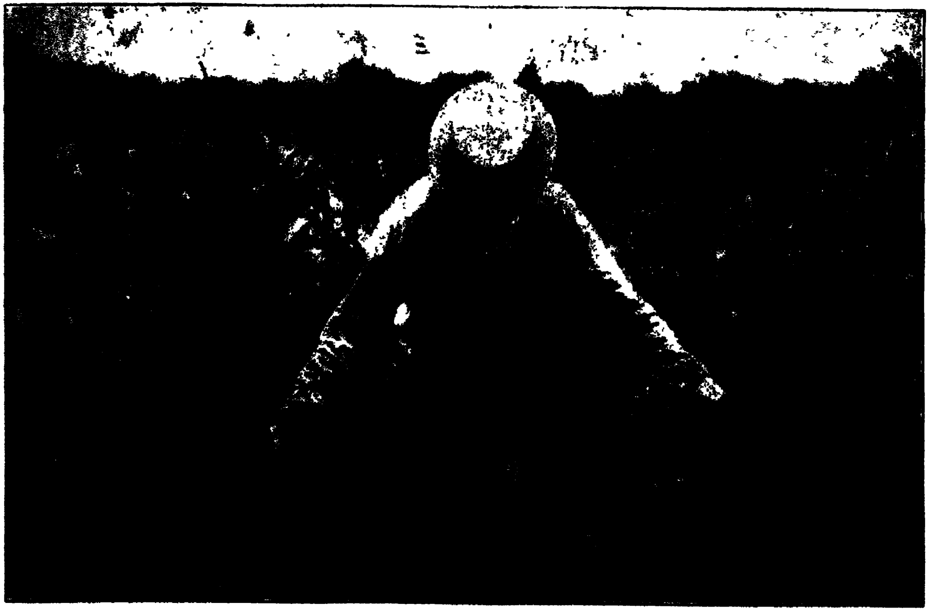


Fig. 30. Strength of individual stalks of corn on the breeding blocks of Funk Bros. Seed Co., Bloomington, Ill.

The use of fertilizers, more careful processes of preparing the land and handling the seed and the plants, and a proper choice of the seed-grain are the acknowledged means by which to attain this end.

Of course, in these lectures I am concerned only with the questions relating to variability and selection. But no crop is more responsive to careful selection of the seed than corn.

According to the condition of the land, the treatment of the field may be of first importance, but good seed will always add considerably to the yield, and the more so, the better the condition of the soil and the care given to its culture.

Some farmers are producing 60 to 70 bushels per acre every year, while their neighbors are contented with an average harvest of 30 to 35 bushels. In favorable cases the product might easily be increased to a hundred bushels per acre and even more.

As a rule, however, the corn yield per acre is gradually decreasing, at least in some of the leading states. In Ohio the period 1890 to 1899 shows a falling off of 3½ bushels as compared with the previous ten-year period. But in Indiana, where the interest in corn selection is rapidly growing, the average yield per acre has increased during the same time by 12.8 per cent, and in Illinois, which has started the principle of individual ear selection, the yield per acre of corn has increased to 22 per cent more than in the ten years preceding the introduction of this new method.

The recent discoveries made at the Agricultural Experiment Station of Sweden will, no doubt, some day exercise a notable influence on the American processes of corn-breeding. In some points they are in full agreement with them, but since they are founded on more elaborate scientific methods, they may facilitate the understanding of the processes now in use.

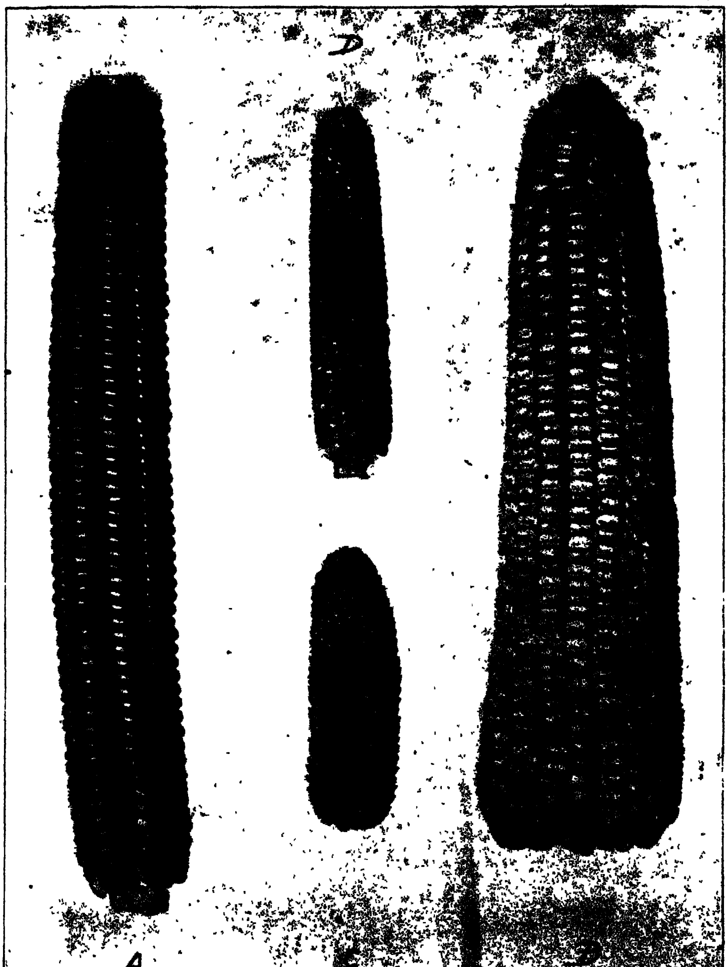


Fig. 31. Different types of corn. A. King Philipp, a variety of flint corn. B. Giant yellow dent corn. C. Rice popcorn. D. Dwarf popcorn.

In some of the bulletins of the agricultural experiment stations, dealing with the improvement of corn, it has been pointed out that we do not yet understand many of the principles underlying corn-breeding, but that on the other hand it is to the interest of each corn-grower to obtain as complete a knowledge on this point as possible, in order thereby to bring the factors of his selection under his control.

From a scientific point of view, however, there can be little doubt that the same laws that govern the variability and the selection of cereals in general control the corresponding phenomena for corn, too, and that the existing differences are, as a fact, only due to those plain and easily recognizable characters which contrast corn with the smaller cereals.

For this reason I propose to give a description of the facts of variability and the methods of selection of corn, based on the principles evolved for cereals in my previous chapters. I shall conscientiously describe the facts, but shall rely in their appreciation partly on the obtained results, and partly on a comparison with the Swedish and German principles. In doing so my chief aim is to awaken the interest of all those who are in one way or another concerned in corn-breeding, for a study of analogous questions in other crops.

The study of variability is the basis of all selection. The more we are enabled to discern slight differences and to appreciate their possible industrial value, the better we shall be guided in our choice.

Moreover, the term variability covers so wide a range of phenomena, and the significance of the single constituents of this large group for the purpose of race-breeding is so widely different, that it is of pre-eminent importance to have a critical survey of the most obvious cases.

Everybody knows that corn is one of the most multifor

Fig. 32. A. Sweet corn, an ear with a staminate upper part and with some few kernels in top. B, C. Parts of a tassel of flint corn bearing staminate spikelets and kernels.

species. It embraces seven types which are different enough to be considered by some authors as the equivalent of systematic species. Each of these groups includes a number of varieties or sub-races, and these, in their turn, are by no means uniform, but offer to the experienced eye an utter chaos of individual variations.

The significance of the main types and their most evident varieties is nowadays fairly well established, but it is the almost inexhaustible individual variability within the varieties that gives the material for selection.

The main types are six in number, viz.: The pod corns, the pop corns, the flint corns, the dent corns, the soft corns, and the sweet corns. In the pod corns or Zea Mays tunicata the kernels of the ear are enclosed in husks, constituting together a pod for each single kernel. This is the form which was assumed by Darwin to be the nearest relative of the hypothetical ancestors of the whole group, since corn is the only species in the family of the grains, which possesses naked kernels.

The pop corn is easily recognized by the small size of the kernels and ear and by the excessive proportion of the horny or corneous endosperm, which, in the best varieties, is so well developed that it wholly excludes the starchy tissues. This gives the property of popping, by which process the kernel is burst and the contents turned inside out. The rice pop corns, with pointed kernels, are among the best-known races of this group.

The flint corns have a well-developed starchy tissue enclosed by the horny endosperm. This latter varies in thickness with the varieties and causes the kernels to become too hard when dry for cattle to eat them without their being ground. Thence, the Latin name "indurata."

The dent corns, Zea Mays indentata, are easily recognized by the indentation on their outer surface. This de-

Fig. 33. A highly ramified ear of corn.

pression is caused by the shrinkage of the starchy matter in drying. The dent varieties are almost the exclusive corn crop of the corn states and are of supreme value in the feeding of cattle; they are more numerous than all the varieties of the five remaining groups taken together.

The soft corns, Zea Mays amylacea, have no corneous endosperm, as their name indicates. The kernels, however, shrink uniformly and do not become wrinkled in drying. This group includes some of the oldest varieties, as, for instance, the mummy corns of Peru and Chile, and the very largest-kerneled type, the Cusco.

The sweet corns, or Zea Mays saccharata, are characterized by their wrinkled and more or less translucent seed. This condition, however, is not caused by the horny part of the kernel, but by the starchy tissue in which the starch is almost wholly absent. It is replaced by a sweet constituent or kind of sugar, belonging to the group of the dextrines. It is mainly grown for table use and for canning purposes, the grain being canned before becoming ripe. Maine and New York are the principal states for this culture, which, however, extends all along the Atlantic coast.

In each of these six main groups there are a number of varieties which are partly distinguished by the forms of the kernels, whether broad or deep, partly by the proportion of the horny and the starchy part of the endosperm, and partly by many other subordinate marks. E. L. Sturtevant, in his Varieties of Corn (U. S. Dept. of Agriculture, 1899, N. 57) enumerates 300 varieties of dent corn, 70 of flint, 60 of sweet corn, and so on. These varieties or sub-races are cultivated under different names, and their characters are said to be constant and more or less sharply defined, not changing under the influence of soil, climate, or treatment. Among the dent corns the dimple-dented, crease-dented, pinch-dented, and ligulate-dented may be cited as instances.

But almost every one of these varieties is all but uniform. They include all kinds of variations, both in the shape of the kernel and the ear, and in the mode of growth and vegetative characters of the stalks and foliage. The differences among these minor types within a given variety are often as great as those which distinguish the varieties themselves. As a fact, the varieties are mixtures of a larger or lesser number of constituents, the same sub-types recurring often in more than one so-called variety.

Moreover, many of these varieties are subjected to abnormal deviations from the type or so-called monstrosities, including the most widely divergent forms. Stalked and branched ears, male side-spikes on the ears, kernels in the tassels, cockscomb-ears, hermaphrodite flowers, variegated leaves, and many other features are the well-known instances. They are without practical value, and their hereditary characters have accordingly been only imperfectly studied. Such study should not be neglected, however, since the barren stalks, which often cause enormous losses, seem to belong to the same group and to obey, in their manner of inheritance, the same laws. But with this phenomenon I shall have to deal later.

The variability within the varieties is the main source of all selection, and, as such, deserves our careful attention. The distinguishing marks are many, but often so minute as to be hardly fit for description. Often they are the same as those between distinct varieties, and in such cases different varieties may simply be different mixtures of mainly the same constituents. In some cases the same varieties may even be cultivated locally under different names. Mixing of color is the easiest indication of such a mixing of sub-types; it has attracted the eye of the farmers for a long time, and often led them to some kind of primitive selection, preferring a pure color to the mixture.

In selection, uniformity is one of the main purposes, but the shape and color of the ears, their butt and tip ends, the number and direction of the rows, the furrows between the rows and many other points have to be considered. It is only by an actual study of these variations that a farmer may become familiar with all the different types. It would be quite superfluous to try to describe them here, the more so as we shall have to quote a number of instances, when dealing with the work of selection.

Perhaps the most important discovery which has been made concerning these minor variations, is that of their constancy. All the kernels of a selected ear have the same qualities, provided, of course, that cross-pollination has been sufficiently excluded. This is easily seen in their visible or physical qualities, but the experiments of Hopkins have shown that the same rule prevails for the chemical constitution, including the relative development of the main industrial constituents. Moreover, it is true for the hereditary qualities.

In the first place, direct experiments have shown that neither the yield nor the quality of the grain is essentially affected by choosing the seed-grains from the butt end, the middle, or the tip of an ear. Furthermore, it is now customary, as we shall soon see, to sow the kernels of selected ears in single rows, each ear to a row, and by this method the fact of the individuality of the rows has become quite conspicuous. A whole row, grown from the kernels of a single ear, may produce numerous barren stalks, or weak plants, or small ears with imperfect yield, or be excellent in strength, productivity, and uniform in other peculiar characteristics. This fact is now the acknowledged basis of the main principle of corn selection.

From these and many other concurring observations we may conclude that the variability of corn within the varieties

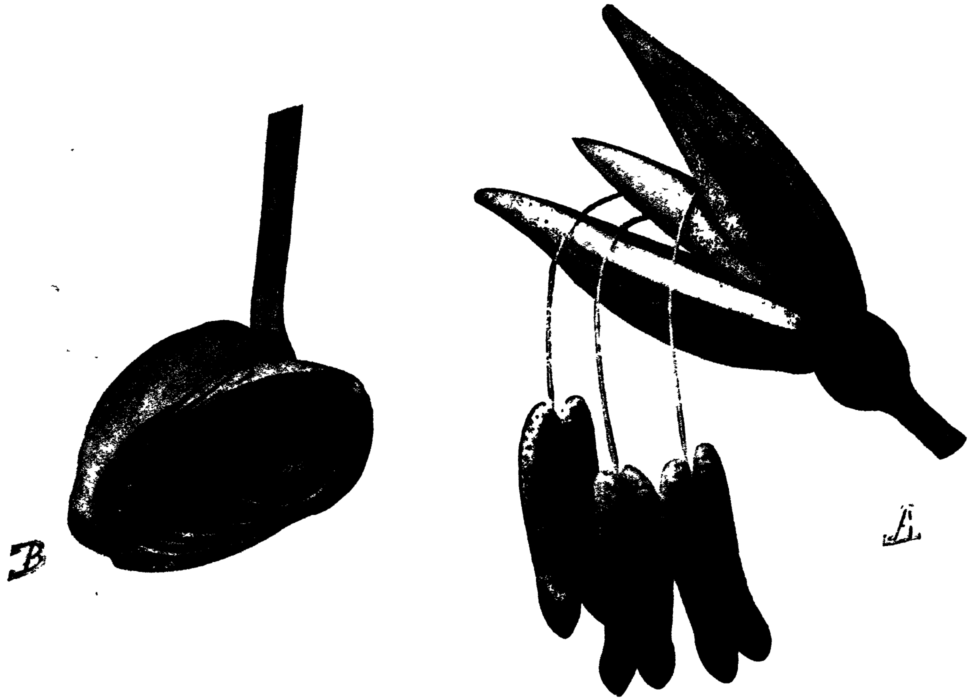


Fig. 34. A. A male or staminate spikelet of corn. B. A pair of pistillate or female flowers. After models of Brendel, Berlin.

mentioned is of the same nature as that observed at Svalöf for the other cereals, and described in our previous lectures. Thus the varieties are to be considered as built up of quite numerous elementary forms, each of which is essentially uniform and constant. The cross-pollination must, of course, obscure this fact to some extent, but cannot annihilate it. As soon as such an elementary form is sufficiently isolated and multiplied so that its progeny may fertilize itself exclusively, a uniform and constant race will be obtained. Variability will then be limited to the smaller, but unavoidable changes, which climatic and environmental conditions will always evoke, even in the most purely bred races. The nature of these so-called fluctuations we shall soon have to consider, but for selection they are only of secondary importance.

The principle of selection at the Svalöf Experiment Station consists in the search for such elementary forms, and in their isolation and subsequent comparative trial. No purifying and no fixing, or in other words, no subsequent or continuous selection is needed, provided the chosen ears are not hybridized. Man cannot originate these variations, nor can he essentially improve them. He must simply be on the alert to recognize and isolate them and to compare their progeny with the main strain. In the same way the problem of corn-breeding is to recognize these elementary races. All success depends upon finding the best among them and on thus taking complete advantage of the variability already existing in the fields. Even the races with special characters, as, for instance, those with a high yield of oil or of protein, have, as a fact, been secured in this same way.

Corn, however, differs from the other cereals in some very important points. Two of them are now to be considered. One is the open pollinized condition, and the other

Fig. 35.* A. Tassel of corn, flowering and producing the anthers from the spikelets. B. Ear in the husks, producing the silks.

is the large size of the ears and their enormous number of seeds.

On a normal individual, the female or pistillate flowers are combined on the ears, and at the time of flowering the pistils or silks are protruded from the top of the husks. The wind has to carry the pollen to them. The male or staminate inflorescences are the tassels on the top of the stalks. Each flower contains three stamens, and each tassel produces about 20,000,000 to 50,000,000 grains of pollen. By far the largest quantity of these is, of course, lost, being deposited on the foliage or falling to the ground. But a sufficient number are transferred to the silks to insure the complete fertilization of the ears. This, however, is not reached at once, but several days are needed for the process. The silks do not all appear at the same time, those of the uppermost kernels being the first. Moreover, they continue growing until a considerable length is reached. The diffusion of the pollen mainly takes place early in the morning, when the scales and anthers open under the influence of the rays of the sun. Four or five days are usually required to pollinate all the silks of an ear.

It is evident that only a part of the pollen will fall upon the silks of the same plant. This is called self-pollination or self-fertilization. The stronger the wind blows, the greater the quantity that drifts to other ears, thereby insuring cross-fertilization. Pollen will drift in this way over long distances, and is known to have been carried by the wind over more than a thousand feet of surface. If kernels of one mother ear are sown close to one another the pollen may be transferred to the children of the same mother, and this is called close-pollination.

The effects of cross-fertilization often can be seen when different varieties are cultivated on adjacent fields. Some color-varieties and the sweet corns are exceedingly liable to

this phenomenon. In these cases the effects may be observed directly on the ears, without awaiting the next generation. This is due to the phenomenon known as double fertilization and which has been discovered only lately. The endosperm, in order to develop, must be fertilized as well as the germ, and this is brought about by the tubes of the pollen grains carrying each two male elements or cells, one destined for the germ and the other for the endosperm. Hence we see that in cross-pollinizing the endosperm assumes a hybrid nature as well as the germ. In ordinary cases this condition does not betray itself by any visible mark. In crossing sweet corn with dent or flint corn, the hybrid endosperm assumes the characters of the male parent. Thus, when an ear of sweet corn is partly fertilized by a dent corn, we shall find on it, after ripening, some starchy kernels among the wrinkled and translucent majority. It is evident that the number of these aberrant kernels will correspond to the number of threads in the silks which are thus cross-pollinated, and the number of the differing kernels is to be considered a direct measure of the proportion of alien pollen

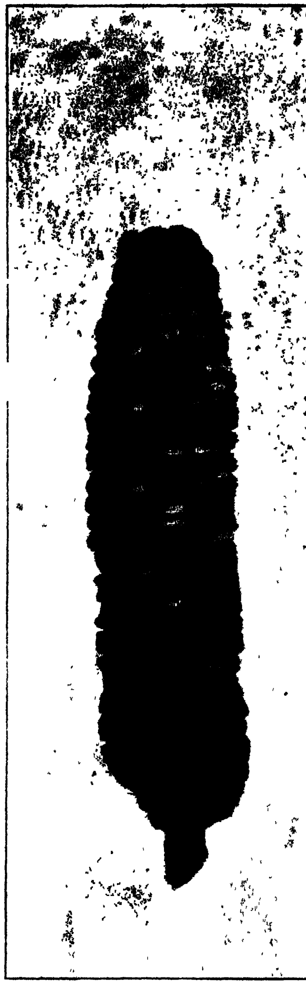


Fig. 36. Sweet corn, with scattered starchy kernels, produced by partial cross-pollination.

deposited on the silk. In close proximity this number will often surpass that of the normal kernels, and by artificial cross-pollination all the kernels on an ear of sweet corn may be induced to become starchy. It is a simple method of measuring the degree of transportation of pollen by the wind, and wherever a field of sweet corn is near a culture of dent corn, the inspection of the ears may give us an idea of the significance of this transportation.

All the starchy kernels on a partly cross-pollinated ear of sweet corn have hybrid germs, since they were fertilized by the contents of the same pollen tube as the endosperm. By this means the hybrid kernels may be recognized and eliminated in such cases, and thus the strains of sweet corn are easily kept pure of admixtures of this kind.

This wind-pollinated condition of corn has a great influence on the process of selection. In other cereals, whenever a single head has been selected in the field, it is almost sure to be exclusively self-fertilized and its progeny will at once yield a pure and uniform race.

In corn, however, a selected ear will almost always be partly cross-fertilized, and probably by the pollen of more than one of its neighbors. If we could eliminate these hybrid kernels and sow only the self-pollinated seeds, we might expect to get at once a pure and uniform race, which would need only careful protection against foreign pollen during the first year of its multiplication. There can be hardly any doubt that this conclusion, drawn from the other cereals, would hold good for corn also. At present, however, it is impossible to distinguish the cross-fertilized kernels of an ear from the self-pollinated seeds, except in such extreme cases as we have just alluded to. The only way is to sow all the seeds, and to judge the plants when growing. In some instances the hybrids may be recognized and thrown out before tasseling, but ordinarily they will have to stand in the field until

Fig. 37. Method of sacking ear and tassel in corn for hybridizing, Agricultural Experiment Station, Manhattan. Kansas

the time of husking. Part of their pollen will be carried to the true representatives of the chosen race, and repeat the mixture of the characters of the paternal and maternal strains.

Fig. 38. The hand pollination of corn in one of the breeding blocks on the farms of Funk Bros. Seed Co., Bloomington, Ill.

It is easily seen that in the ordinary process of selection, the result of this open fertilizing condition must be that the choice is partly initial and partly repeated or continuous. The initial choice is the main one on which almost all further success depends, but the repeated choice gradually eliminates the bad effects of the unavoidable cross-fertilization of the first chosen ear. The initial choice corresponds to the Svalöf method but the subsequent repeated choice can be compared with the German method, as described in my previous chapter.

Or to put it in other words, the pedigree on the female side is pure and fully known, but on the male side it is impure and only vaguely known and must be purified by repeated selections. Fortunately in practice this difficulty is not so great as it might seem to be, for experience shows that as a rule there is a great uniformity in the progeny of a single ear,

even if this is chosen from an ordinary unbred variety. On the other hand, as we shall soon see, great care must be taken in order to make sure that after the first selection all the sires of the selected ears are as superior plants as the chosen individuals themselves.

After having discussed the effects of the wind-fertilizing conditions of corn, we have now to consider the influence of the large size of the ears and the great number of their kernels. This character makes the comparing of corn ears far more easy than that of heads of any other cereal. The qualities are more easily appreciated, and the multiplication being so much faster, the importance of the work is greater. At the time of husking, the ears have to be handled singly and this will favor their inspection and study. Seed corn has to be as uniform as possible, and the easy inspection of the ears will lead to the elimination of all those ears which do not comply with this condition, even in a pure race.

We may assume that pure races of corn, derived each from a single purely fertilized ear, will show some degree of variability, and that this multiformity will strike us as more important than in the case of smaller cereals. With the same degree of variability the smaller ears of wheat, with their minute differentiating marks, will seem to be more uniform than a strain of corn, in which the differences are so much more visible to the eye.

It is the ordinary or fluctuating variability with which we have here to deal. It embraces the effects of environmental conditions on the plants, in the growing state as well as during the ripening of the germ of the seed. In the more striking cases these effects are well appreciated even by ordinary farmers, and some instances may be adduced: Good qualities may be due to accidental advantages, caused by deficiencies in the neighboring plants. Whenever the neighboring seeds fail to germinate, or when by some accident the

young plants are checked in their development, the remainder will have more space, more sunlight, and more plant-food than usual. Everybody knows that ears which have profited by such exceptional circumstances, are no true representatives of their race and cannot be relied upon for seed corn. Their excellence is not due to inheritance, they are only personally superior without promise of an improved progeny. Other ears may fall back from the average by reason of unfavorable conditions, without having less value as seed corn. It is a most interesting fact that often two ears, especially when gathered from selected strains, apparently may be exactly similar and notwithstanding this, give a very different progeny when tested separately. It shows that there is a kind of variability which has no direct relation to inheritance, at least, not in the ordinary sense of the word. It does not lead to racial improvement. Very little is known, as yet, concerning the significance of the deviations from the average type, which purely bred strains of corn may produce by this unavoidable and inexterminable kind of variability. We can state only that the characters of the single ears of a pure race will differ somewhat from one another. The characters are oscillating around the mean condition in correspondence to the more or less favorable life-conditions of the single plants. According to our experience with other plants, the deviating ears of a pure race may possess the power of transmitting the good yielding qualities of the strain to the same degree as the average specimens. But, of course, in practice, they can hardly be relied upon on account of the always possible contaminations by foreign pollen. In all cases where the uniformity of the ears and the kernels is showing such fluctuating variability a choice of the best ears will have to be made. But this choice is made in the interest of a regular planting and a normal stand and not of a racial improvement by selection. It is difficult to appreciate the dif-

Fig. 39. Another view of hand pollination in breeding-blocks of corn of Funk Bros. Seed Co. Bloomington, Ill.

ference between the variability among the races and within the races themselves, and only a comparison with the phenomena observed in other plants will lead to a clear and useful distinction.

The history of the breeding of corn is a very short one. It dates from the discovery of the principle of single-ear selection, ten years ago. The observation of the individuality of the progeny of one single ear is the basis of this method. It enables us to estimate the hereditary value of an ear by the inspection of its progeny. It is in full accord with the methods of Hays and Von Lochow, who applied them to wheat and rye, and with the Svalöf method. It is different from them only on account of the impurity of the fertilization of the selected ear, as we have already described. Since the discovery of this principle of single ear selection, corn breeding has rapidly developed and it is now holding a pre-eminent place among the methods of increasing the yield of this valuable crop.

Previous to 1897, little was done in the way of breeding corn systematically. It is even as in the case of the European cereals, where but few farmers had the idea of improving their crop by selecting their seed, and became the originators of some few ameliorated varieties. But they did not attain to any influence upon the farmers at large. Working only for the improvement of their cultures, they failed to persuade others of the validity and the importance of their views.

Among these men J. L. Leaming, of Wilmington, Ohio, began his work about 1825. He simply selected the best ears of his field for his seed corn, and in doing so he soon improved his strain of corn to such a degree that other farmers secured his seed-corn for their own farms, and it was soon imported into Illinois. There it has since been improved by subsequent repeated selection, and the Leaming

variety is now considered one of the best yielding sorts of this state. Half a century afterward, in the year 1875, another farmer applied the principles of cattle-breeding to his corn. James Riley, of Thorntown, Ind., selected seed from the ordinary white corn of Indiana in order to diminish the number of barren stalks and of ears of minor value in his fields. By this means he isolated a variety which he called Boone County White and which is now the most popular variety of white corn in Indiana and Illinois. It is one of the best yielders.

It would be superfluous to enter into more details. Some crude attempts at selection, as, for instance, the separation of kernels of different color, have been almost universal. Besides these, the comparative testing of different commercial varieties has long since been the acknowledged means of securing the types which best responded to each special local demand. Much improvement has been obtained in this way, but in the long run it has not been adequate to comply with the increasing necessity of keeping up with the exigencies of consumption and industry. It is only since the discovery of the prominence of breeding from single ears that a start has been made that seems destined to change the whole aspect of agriculture in the corn-breeding states.

The man who started this new principle was Dr. Cyril G. Hopkins, Professor of Agronomy in the University of Illinois. He proved the individuality of the ears not only for the physical characteristics of their kernels, but also for their chemical qualities. He showed that corn may be bred by selection not only for yield, but for special characteristics and value for different industrial purposes. He succeeded in convincing the farmers of Illinois of the great possibilities of systematic selection and improvement of corn. The result has been the organization of a society for the purpose of putting corn selection on a business basis.

The Illinois Seed Corn Breeders Association was organized in 1900, and began its work in 1901. Soon afterward, similar associations were organized in other corn-breeding states, and the systematic production of selected seed is rapidly gaining sympathy among the farmers throughout the United States. In the corn states it is, of course, the dent corn with its numerous varieties which must be ameliorated, but in Connecticut, Maine, New York, and other eastern states the flint corns and the sweet corns are equally in need of improvement. Farmers are now almost everywhere willing to pay higher prices for pedigreed seed-corn, although these commonly average double the value of ordinary seed. Corn breeding has become a prominent part of the work of many of the agricultural experiment stations, as well as a special business for some large firms. Prof. P. G. Holden, of the Iowa State College of Agriculture, at Ames, Iowa, has brought the work of that station to the front rank, and the Funk Brothers Seed Company, at Bloomington, Ill., are pushing the selection of corn as a business enterprise to its highest possible development.

As a rule seed-corn has to be purchased on the cob, although the price is often nearly double that of shelled seed-corn. In Illinois the price of a bushel, for the best varieties, is in the first case $3 (70 pounds of ears), and in the other case $2 (56 pounds of shelled corn per bushel). The quality of the individual ears is a criterion of the choice condition of the crop and a guarantee for the next generation, but the purity of shelled corn can never be wholly relied upon. No seed should be imported from distant localities, except for the purpose of experimental trials. Ordinary unbred varieties, which consist of mixtures of minor types, will, as a rule, change during the first years after importation, some of the constituents gaining and others losing in their proportionate part of the harvest. Of course, such

changes can never be accurately predicted, and therefore the value of an imported variety can be determined only after the change has been completed. Northern varieties are, as a rule, shorter lived than southern forms, and this is one of the main reasons why the common belief of the great profits being secured by bringing in seed from other localities is unfounded. When one goes south for seed-corn, he is apt to get a variety that will not mature in his locality, and northern kinds will easily prove, on introduction, to mature too early and to yield a correspondingly small crop. As a rule, every degree north or south of a given locality means eight or ten days difference in the time of ripening. No farmer can depend on imported seed for his main crop. He may purchase it for his breeding plot, but he may as well select the best ears from his own fields. All trouble incident to imperfect adaptation to the local conditions of soil and climate can be avoided only in this way.

I am now coming to a critical description of the actual process of corn breeding as it is performed by the majority of the intelligent farmers of the corn states. I must, however, limit myself to the main method, which, of course, is subject to many changes on subordinate points, according to the special demands of each different locality.

Three main points in this process have to be considered separately:

First.—The initial choice of ears in the field.

Second.—The comparative trial of the progeny of these ears on a breeding plot, during the summer subsequent to the year of the initial choice.

Third.—The continued selection and improvement of the chosen strains.

The full appreciation of these three constituents of the breeding process as different processes will probably, some day, prove to be the most reliable basis for the further

development of the practical methods of breeding. For this reason I will now discuss them as independent processes.

Corn should be selected in the field. Early in the fall, shortly before the time of harvesting, the farmer should go through his fields and mark the stalks of superior quality. Width of blade, indicating a rich foliage as the source of the organic constituents of the seeds, ears borne on shanks neither too long nor too short, and on an average height above the soil and other essential qualities should decide the choice. At the time of husking, the ears of the marked stalks are harvested separately, for the ultimate selection. Since it is impossible to predict exactly the value of the progeny from the inspection of the parent plant, it is desirable to collect as many different types in the field as possible. Their real worth can be determined only in the next year. But the selection of that year will evidently be limited by the choice of the first year, and the wider this choice is, the greater are the chances of ultimate success. Of course, no farmer will select plants or ears of minor value, but he should not try to select according to definite conceptions of good qualities, but simply try to collect as many different types as possible, leaving the decision concerning their hereditary worth to the next season. As soon as he has exhausted the whole range of the elementary constituents of his varieties, no further field selection can be of any use, but as long as this limit is not manifestly reached, the fields contain possibilities, which should not be neglected. In ordinary cases it will therefore be profitable to repeat the field selection during some years.

Selection of corn is very easy, when compared with the work connected with the selection of other cereals. The different marks of the stalks and foliage, of the shanks of the husks, of the ears and the kernels, are easily appreciated, and their significance for the value of the new strains is mani-

Fig. 40. Growth of individual rows of corn on the breeding blocks of Funk Bros. Seed Co., Bloomington, Ill.

fest. Each farmer can gather the knowledge and experience, which this process requires, and a few days' work in a season may secure great profits without any notable outlay. Of course, the greatest profits will come to those who have a taste for the work and are willing to give it the necessary attention. The most successful farmer is the one who adopts scientific as well as practical business methods, and who is guided in his breeding work by a thorough knowledge of the laws of variability. He must be prepared to discern the direct effects of environments from the marks of hereditary qualities. He has to appreciate slight differences, in the hope of seeing their significance increased by the culture of the next year. By breeding, the yield per acre can easily be increased by five bushels, and it is evident that this increase is pure profit to the grower.

The field selection is, however, only preparatory work. The real selection is obtained by the comparison of the progeny of the chosen ears. All selection must be based on performance, since the aim of the work is the improvement of the hereditary qualities. Many an ear has been found of excellent shape and size, with straight rows and perfect butt and tip, with most uniform kernels of the most desirable structure, but it has been rejected, because it lacked the power of transmitting these qualities to its progeny. Often of two ears chosen in the field, and exactly similar in all respects, the one has given a generation which yielded double the harvest of the other. The propensity to produce barren stalks cannot be judged by the inspection of the ear, but it becomes manifest in the generation cultivated from its kernels. Many other instances could be given, and all of them will point to the same conclusion, that the hereditary qualities of an ear are a character which demands special investigation. This investigation is the separate culture and exact comparative trial of the generation grown from its

kernels. It is exactly the same principle which now prevails in the work of the Swedish Agricultural Station at Svalöf.

The comparative trial of the progeny of the ears selected in the field is made on a separate field plot, which is usually called the breeding plot. Every corn grower should have such a breeding plot. Here the grains of each ear are sown in groups, so that it may be easy to compare the different groups with one another. Two methods have been proposed, the row system and the plat system. In the first, the kernels of one ear are sown on a row by themselves, the second row containing the progeny of a second ear and so on. By this means the comparison of the rows is the basis of judging the mother ears. Experience has shown that this system is the most convenient, and it is now generally in use. It is, however, exposed to the maximum degree of cross-pollination and this must manifestly affect the purity of its harvest. In the system of breeding in plats, the progeny of each selected ear constitutes a square by itself, and thus at least for the central stalks a high degree of pure fertilization by the other members of the same family is insured. The observed fact of the high degree of individuality of each family, derived from one single ear, seems to point out the desirability of this plat system for the first year of trial on the breeding plot, even if the row system should be kept as the most convenient for the subsequent years of selection. The experience gained at Svalöf would justify the expectation of a considerable shortening of the number of years, required to reach the limit of possible purity, by the adoption of the plat system for the first year of comparative trial.

A breeding plot usually embraces about 100 rows, each derived from one mother ear, and in each row about one hundred hills, planted with three seeds each. At husking time each row is harvested separately and the total weight of its ears is the main factor of the comparison, since aug-

menting the yield is the most essential purpose of all breeding. The comparison, of course, suffers from the cross-pollinated condition of the mother ears, but, as we have seen, as a rule, not to any noxious degree, and the plants grown from such hybrid kernels will probably be thrown out by the first selection. The plot should be protected as effectively as possible from contamination by pollen from unbred varieties. As a rule, it will hardly be possible to place it on good soil at a sufficient distance from the remaining fields, and a protection by hedges or timber will equally be too cumbersome in ordinary cases. The best plan is to place it in the midst of a large field of a selected strain and to surround it by three or more rows, sown with the seeds of the selected ears which remain after the preparation of the seed corn for the main rows. The first contrivance will, of course, not be available in the first season after starting the breeding plot, but from the third year it will always be practicable. In the choice of the best place, attention is to be given to the direction of the prevailing winds, that they may carry as few pollen grains from the adjacent fields as possible. It has often been ascertained that pollen has drifted over a quarter of a mile, and by the planting of stray plants of sweet corn and the estimate of the number of starchy grains produced on them, some knowledge concerning this transportation of pollen could easily be secured. Dr. Hopkins has pointed out the dangers of repeated self-pollination in the breeding plot and recommended the detasseling of alternate rows and the harvesting of the ears of these rows only, in order to meet this difficulty, but with this question we are not here concerned. In the first breeding year close-pollination of the progeny of the same mother ear should be appreciated as a means of shortening the period of subsequent selection; it will probably prove harmless even if a repeated close or self fertilization should prove objectionable.

The best ears of the breeding plots are divided into two groups, the very best of which is destined for the breeding plot of next year, and the other for the multiplying or increase field. Here it is cultivated and multiplied in order to yield, in one year, all the seed corn for the commercial fields of the farm. By this means well bred seed is secured for the main crop of each year from the breeding plot of two years before,

Fig. 41. Rows from ears of corn which have been self-fertilized and from those which have not been self-fertilized. The small rows are those self-fertilized. On the breeding blocks of Funk Bros. Seed Co., Bloomington, Ill.

either for ordinary purposes or eventually in order to sell the product of the farm as pedigreed seed-corn.

The selecting work on the breeding plot can be divided into two parts, that before and that after tasseling. The first comprises all those characters which may be judged on the growing plants; the second is mainly concerned with the ears themselves. The first is accompanied by the extirpation or detasseling of all the stalks which at that time prove to be of minor value and so prevents them from cross-breed-

ing into the remaining plants. Otherwise, at the time of husking, the ears will have been partly cross-pollinated, and no account can be taken of this in the selection. The judging and elimination of its effect must then be left to the next season.

From this discussion it is manifest that all selection which can possibly be performed before flowering should be done at that time and be accompanied by the detasseling of

Fig. 42. Alternate detasseled rows of corn, at a later period of growth on the breeding-blocks of Funk Bros. Seed Co., Bloomington, Ill.

the inferior stalks. This detasseling is done by pulling the tassels out and is without injury to the plant. It requires going over the field at least three times, in order to pull out the tassels of all the imperfect plants, when they are fully developed, but before the opening of the anthers and the spreading of the pollen. No plants which appear broken, dwarfed, immature, barren, or otherwise undesirable should be allowed to mature pollen. The occurrence of tillers or suckers and other characters can be attended to. Rows

of general inferiority should be detasseled as a whole, since in such cases it is manifest that the whole family has an hereditary tendency to become imperfect.

The main point, however, in the selection before tasseling is the occurrence of barren stalks. Barren stalks are plants which do not produce a fertile ear. As a rule they have imperfect ears and more or less developed tassels. It is generally surmised that this barrenness is hereditary, although to a large degree it is dependent on climatic conditions. As a matter of fact, seed-corn which has been fertilized by pollen produced from barren stalks is liable to give rise to an increased number of useless plants. In many cases the number of barren stalks reached as high as thirty per cent, and it is evident from this that they are one of the greatest sources of loss in corn growing. They are even worse than a simple loss of that amount, since, except for detasseling, they deteriorate the quality of the neighboring ears as seed corn by their pollen. But a little care in selecting will materially lessen this enormous loss. The method of breeding the seeds of single ears in rows has proved that different degrees of barrenness are inherent in different families. Some ears produce more than twelve times as many barren stalks as others, and for broken stalks a similar rule of family individuality prevails. Hence it is clear that rows which are marked in this deficiency should be detasseled as a whole, and that their ears should be excluded from the ultimate selection. Only strains with the smallest possible propensity to barrenness are worth cultivation. By following these rules the per cent of barren stalks has been greatly reduced. For instance, in Illinois, on farms where this number reached as high as about sixty per cent, it has been reduced by selection, in the lapse of five years, to about ten or fifteen per cent.

The high importance of the combating of this evil may

justify a discussion of this principle from a scientific point of view and a few suggestions upon the great superiority of the row system of testing. The main point is to support the view that the detasseling of the barren stalks themselves is only a very imperfect method, but that the same treatment of the whole rows is what is absolutely necessary, the pollen of the normal plants of such rows being as dangerous as that of the barren stalks themselves. My suggestions are based partly on my own experience with a special kind of barren stalks, which produced neither ears nor tassels, and partly on my experiments with other kinds of monstrosities in other plants. For barrenness is to be considered as a monstrosity, which, like all other monstrosities, is inherent in a race, but is developed only in a certain percentage of its individuals. The same monstrosity may occur in some races only in a small per cent, being found in other strains of the same variety in as much as 30 to 40, or even 50 and more per cent. Evidently this holds good for barrenness in corn, too, and the families with 30 to 50 per cent are those which must be eliminated by selection, while only those with a small per cent may be multiplied until the time that strains will be discovered without any propensity to this deviation. Ordinary monstrosities can be propagated, in scientific experiments, as easily from the self-fertilized seeds of the completely normal individuals as from the seeds of the monstrous plants. There is no difference in the quantity of the deviating specimens of the progeny between these two sources of seed, the normal plants being as liable to give a monstrous progeny as the monsters themselves.

Some instances may be adduced. Torsions are of quite common occurrence among teasels. I isolated a family which produced yearly, during a long series of its biennial generations, from 30 to 45 per cent of twisted stems. In 1900, I protected the twisted specimens from the pollen of the

Fig. 43. View in the Experiment Garden of Amsterdam, with cultures of corn and Evening Primroses.

normal ones and these from the pollen of the monstrous individuals and saved and sowed their seed separately. The seed of twisted origin produced 41 percent of abnormal stalks, the control seed giving 37 to 44 per cent of twisted plants.

Fig. 44. Twisted stems. A. Of a horsetail (*Equisetum Telmateja*). B. of the wild teasel (*Dipsacus sylvestris*).

Ribbon-like stems or fasciations are another hereditary monstrosity. In such a race of the hawksbeard I isolated the normal plants from the flattened stems and gathered the seed separately. The first gave 20 per cent, the latter 20 to 40 per

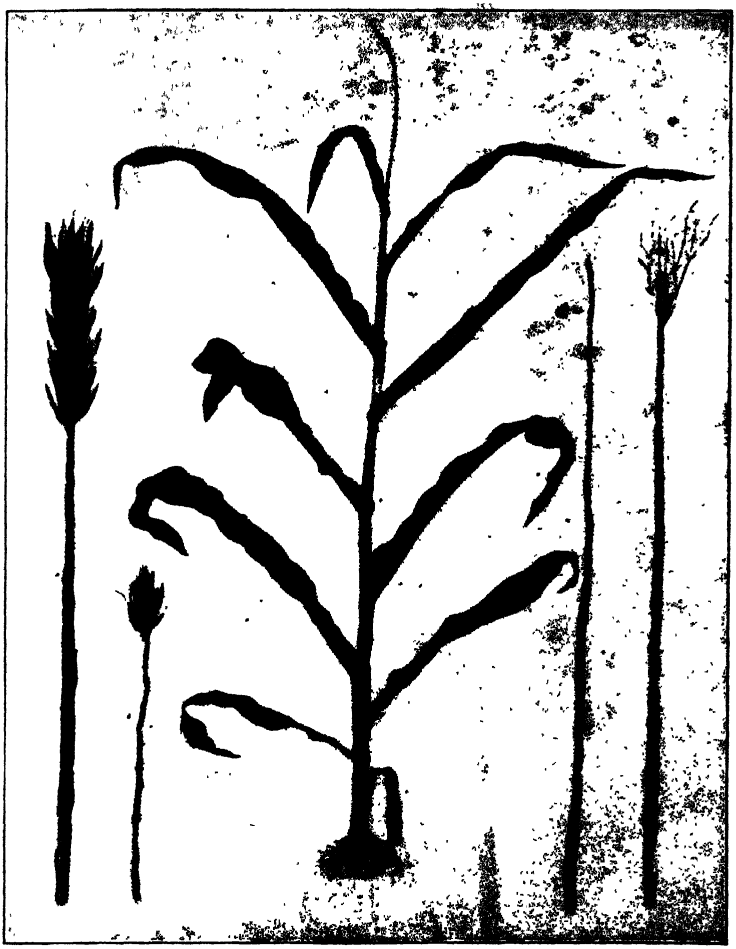


Fig. 45. Sterile corn, a special form of barren stalks without tassel and without ear. Originated in the botanical garden at Amsterdam, 1888.

cent of fasciated stems. Three seed-leaves on a germinating plant of some dicotyledonous species are inherited in the same way and so are connate seed leaves. Of the latter I tried the Russian sunflower, of the former some evening primroses, and quite a number of other species. As a rule, the seeds of normal plants which in their youth had two free seed leaves gave, after pure fertilization, the same per cent of monstrous seedlings as the pure seed of the best selected deviating specimens. Hence we may conclude that in races which contain some kind of deviation, this is as likely to be reproduced from the seeds of the normal plants as from those of the monstrous specimens. Applying this rule to barrenness in corn, we may assume that the fertile stalks of rows which are rich in unfertile plants are as liable to deteriorate the neighboring rows by their pollen as the barren stalks themselves.

It has been claimed that the tendency of Nature is to breed the barren stalks out, even without the intervention of man. This is evidently false. Even if the barren stalks were as deficient in their tassels as they are in their ears, the laws of nature would not lead to any extirpation. Year after year they would be reproduced by the fertile plants which are derived from the same mother ears, and on the average, probably in the same numbers. This conclusion is supported by the evidence of my tasselless barren corn, which has been reproduced yearly from the fertile specimens of the strain, during the years of my experiment. All these experimental facts go to prove that the detasseling of barren stalks is always only a half-measure, the rejection of the entire rows being the only reliable process.

The main work of the comparison of the individual rows is generally done at the time of harvesting or shortly before, while the plants are ripening in the field. Strong and vigorous stalks of medium size, tapering gradually to the tassel, with the ears at a convenient height and having shanks of

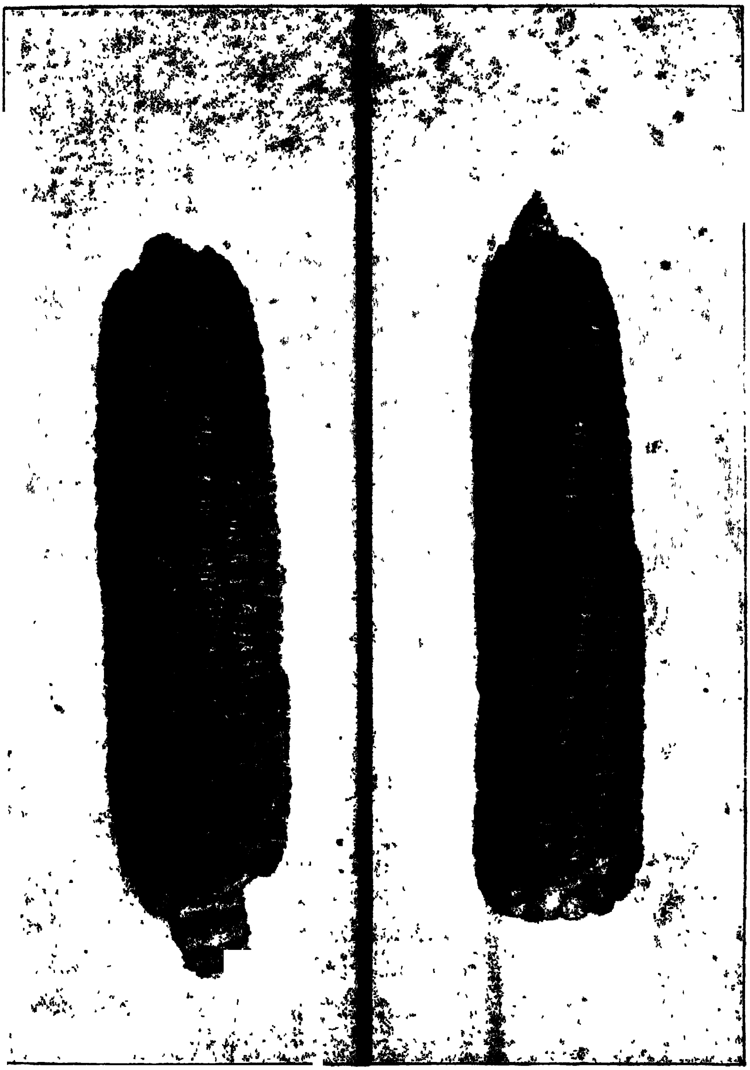
medium length, should be chosen. High ears tend to mature later, too low ears indicate earliness in silking. Flowering before or after the main period of tasseling, they are disposed to be fertilized only incompletely. In a good stand all the stalks should silk at the same time. A short shank holds the ear too erect, while a long shank allows it to hang over too far and exposes the plant too much to heavy winds. Moreover, the long shanks are inconvenient in husking. The suckers, the amount of leaves, and the growth of the brace roots must be considered. The time of ripening and the number of ears on each stalk afford further differences. Plants which may have profited by accidentally good conditions, must be excluded from the comparison since they will probably not be able to transmit their exceptional qualities to their descendants.

Records must be made for each individual row, concerning these and other valuable characteristics. The main point, however, is the total weight of the ears of a row. It must be determined at harvesting time. It is the one great factor of selection, since increasing the yield is the main purpose of the work. Of course, the rows have to be of equal length, each planted with the same number of kernels, but if this condition is fulfilled, the total weight of the ears is the primary factor in determining the best rows.

After the husking, the characteristics of the ears and the kernels should be considered. The comparative value of the kernels depends partly on the demands of the planter or planting machine, partly on their qualities for industrial purposes. No planter can drop kernels evenly, when they are of different sizes and shapes. Experiments with mixed seed have always given an unsatisfactory stand, and only perfect equality of kernels insures a perfect stand. Therefore, the ears must be judged after this mark in the first place. Tapering ears may have smaller kernels on the top

end. The rows must be straight and uniform, their number must be the same over the entire length of the ear. Deviations from these rules will always result in insufficient equality in the grains of the seed-corn. The butts and tips of the ears must be as regular as possible. Rough ears of medium size with a large number of rows of kernels weigh out the most shelled corn. The rows should fit together closely and leave no furrows between them. The best kernels are full and plump at the tips next to the cob and have large germs, indicating high feeding value. The edges should be almost straight in order to fill out perfectly the available space. The cob must be of the same color as the kernels, especially in white varieties, since it is impossible to remove small particles of the cob, and if the cob is red, the meal will be discolored. Last, but not least, the vitality of the seeds must be tested. This is a simple test but of the highest importance, which even in ordinary farming no farmer can afford to neglect. Out of a hundred seeds at least 93 to 95 should germinate. With a lesser degree of vitality the stand in the field would be very imperfect, since each failing seed, of course, causes the loss of a stalk and an ear. Perfect vitality insures a full stand and manifestly has the greatest influence on the yield of the field. In many bulletins great stress is laid on the rule, not to spend time on fancy points. These are characters of the ears and kernels which make a deep impression on inspection but which have no relation to hereditary qualities, or for which at least such relations have as yet not been proven beyond doubt.

After all these and many other points have been considered and duly registered, all is prepared for the final selection. Here the main point is that the rows should be considered as individual families and that the best rows must be chosen. No individual excellence of single plants has any hereditary significance if they are growing in rows of less



A. B.

Fig. 46. Sweet corn. A. With straight rows. B. With oblique rows.

than average value. The entire breeding plot has been started with the purpose of comparing the hereditary qualities of the mother ears, and in estimating the result one should stick to this principle. Excellent specimens in bad rows may owe their qualities to cross-fertilization of the seed from which they sprang, or to accidentally good environmental conditions during their development, but in both cases they have to be rejected.

Next comes the question, how many rows should be selected for the continuance of the breeding culture? Of course, only one of them can be the very best, and if it were possible to select this without mistake, there could not be any doubt about the validity of the principle of choosing one single row. But the experience of the Svalöf Station shows that even for the ordinary cereals such a definite judgment can but rarely be obtained by one year's trial. In compliance with these considerations, practical corn breeders usually choose ten champion rows and start the breeding plot of the next year with their seed. Records are kept and the origin of the mother ears of each new row can be traced. By this means a comparison of the hereditary qualities of the grandmother ears will be possible, and this will prove to be very helpful in the selection of the second year. A most complete analogy with the Svalöf method will thus lead to correspondingly valuable results.

Concerning continuous or repeated selection, many corn breeders in the United States have the same views as the German breeders of wheat and other cereals. They surmise that by careful, continued selection, definite characters can be bred into the strains, according to the wishes and needs of the farmers. This is the theory of slow improvement, which has obtained such a large influence since Darwin built upon it one of the main supports of his doctrine of evolution. In the case of the rye of Schlanstedt, described

in our last chapter, I have pointed out how ignorance of the real nature of the variability of cereals has deluded its originator. It made him assume that a slow improvement was the effect of his twenty years of selection, but in reality he simply gradually isolated by it one of the constituents of his initially selected but mixed group of ears.

According to the experience of the Svalöf Station, no such slow improvement really occurs, and a single choice of an ear followed by a separate culture of its grains is always sufficient to secure a pure and uniform strain, provided that cross-pollinations do not interfere with the result.

These principles must be applied to corn breeding also. Any selected ear will give, in its progeny, a pure and uniform race within the limits of its fluctuating variability, provided that it has not been contaminated by crossing. Here we meet with the main difference in the breeding of corn and of other cereals. With the latter cross-fertilization is an exception; with corn it is the rule. This explains the necessity of repeated selection of corn without having to assume the hypothesis of slow improvement. Repeated selection is the only practical means of eliminating the effects of previous crosses. It is only apparently a fixation of the characters of the young family; in reality it is only its purifying from vicinistic impurities. It is enforced because of the conviction of the detrimental effects of self-fertilization in corn, but if experience should prove that one year's self-fertilization is sufficiently harmless, the process of corn breeding could be shortened in the same way as the Svalöf method may be considered as a shortening of the older processes of breeding of cereals. An experimental test of the value of the Swedish principles in their application to corn breeding would, no doubt, elucidate many as yet doubtful points, and probably lead to some essential changes in the practical work.

Until now I have almost exclusively considered the selection of corn for yield. But since Hopkins has discovered that definite chemical constituents of the grains can be improved also, the selection of corn for special purposes has gained a noticeable significance. Of course, the augmentation of the yield of shelled corn per acre will always be the main care of the farmer, but the glucose factories and the hominy mills will pay a higher price for corn that has been improved according to their special industrial interests.

In order to understand how this aim is reached, we must first consider the structure of the kernels and the relative proportions of their different parts. The kernel consists of the germ or chip and the endosperm, enveloped by a very thin covering called the hull. The endosperm consists of the starchy and the horny parts; its outer layer, of the thickness of one cell, is the glutinous tissue, which may be considered as an inner covering and is usually much thicker than the hull. The size of the germ and the relative proportion of the starchy and horny parts of the endosperm constitute most valuable varietal characters. In the starchy endosperm the tissue surrounding the germ at the tip end of the kernel is called the tip starch, the name of crown starch being given to the starchy tissue at the upper end. These parts are different in their chemical constitution. The oil is mainly produced in the germ, and the protein mainly in the horny endosperm. The better developed these two parts are the richer the kernel will be in oil or in protein. The germ contains 35 to 40 per cent of oil or from 80 to 85 per cent of the total oil content of the kernel. The horny endosperm contains much starch and about 10 per cent of protein, a figure which is variable according to the varieties tested.

From this description it is easily seen that a selection

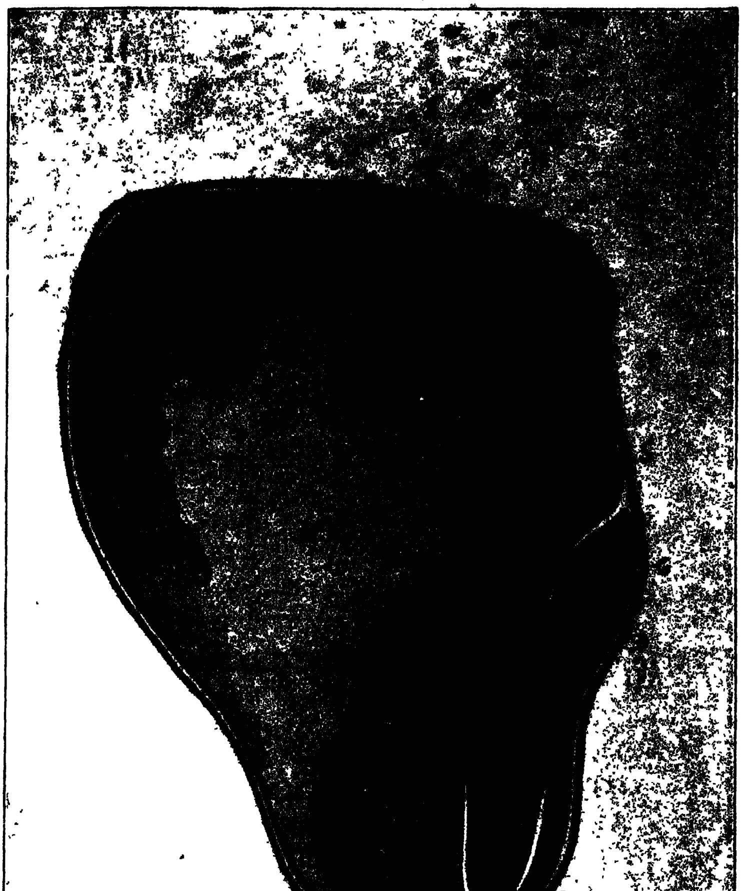


Fig. 47. A kernel of corn cut longitudinally. H. E. Horny endosperm. M. E. Mealy or starchy endosperm. S. Scutellum. G. G. Germ. B. The young bud from which the stem will develop. R. Rootlet. After Frank.

for oil content may be made by the choice of ears with the largest germs, and for protein by the selection of ears with a well developed horny endosperm, or, since the white starch is more striking to the eye, with a lesser development of this tissue, which is poor in protein. This deduction has been confirmed by the brilliant discoveries of C. G. Hopkins, of the University of Illinois, by chemical analysis as well as by direct breeding experiments. In the year 1896, he began the breeding of corn with the idea of changing its chemical contents in an experimental way, and selected seed of white Illinois corn for four different purposes: High and low oil content and high and low protein production. In the year 1903 he had succeeded in isolating four different races, the average values of which differed greatly from that of the variety from which he started. The ears with the extreme percentage of these substances have been picked out by a chemical analysis of two longitudinal rows of kernels for each ear, but their breeding ability has had to be studied in their progeny by the row-system, as described above. The result was the isolation of high and low oil races, which averaged 6.96 and 2.62 per cent, and of high and low protein races containing 14.13 and 6.98 per cent. It is evident that by these most remarkable experiments the possibilities of the breeding of corn for special purposes has been demonstrated, and the value of this fact for large industrial concerns can hardly be overestimated.

For experimental tests and commercial purposes the different parts of the kernels can be more or less accurately separated. This is done by softening them in water and then passing them into mills. First the hull is removed, the germ is freed and the starch body broken up. Water being used, the germs, which are lighter in weight, rise to the surface and are separated. The remaining mass is once more milled or ground and brought into a very fine condi-

Fig. 48. One of the breeding blocks of corn, which is being bred for high protein on the breeding blocks of Funk Bros. Seed Co., Bloomington, Ill., Sept., 1906. To the right, Mr. J. Dwight Funk, explaining his experiments to the author of these essays.

tion. By means of silk bolting cloths the hull or bean is sifted out, and the starch, which is heavier than the gluten, sinks to the bottom. Starch is the basis of a large number of products, as for instance, glucose, grape-sugar, dextrine, and gum. Among them, glucose is the most important, next to the starch itself. The oil is isolated from the germs by pressure after drying and grinding them to a fine powder. The residue constitutes the corn cake and corn meal which is used for feeding live stock. The oil itself is used by paint manufacturers, soap makers and for the production of rubber substitutes, among which the corn rubber or vulcanized corn oil is one of the most important. The hominy mills separate the hulls and germs from the hominy, which chiefly consists of the horny part of the kernel, with more or less adhering starch. Separated in pure form and reduced to a coarse powder, the hominy is called grits, the white starch being put on the market as corn flour or break flour.

The increase of protein is of high value, inasmuch as corn is relatively deficient in this substance and not a satisfactory food for young animals, except when fed in combination with other nitrogenous feeding stuffs. Protein is several times higher in price than corn itself, and consequently the stock feeders want varieties which are richer in protein than the present ones. Any increase of the protein content by selection will make corn more valuable as a food for live stock. It is easily seen that even a slight improvement in this direction would be of tremendous importance. And in the same way there now exist markets for many different kinds of corn. Besides the products already named, whiskey, commercial alcohol, cellulose for coffer dams in battleships, smokeless powder, and many other commodities are manufactured from corn. But since by far the largest quantity of corn is fed to cattle and other meat-producing

animals, the main purpose of the farmer must always be, next to the increase of yield, to improve the protein and the oil. For, to put it in a few words, protein is a muscle former and oil is the fat producing material. From this point of view corn breeding should always embrace both quantity and quality.

Corn breeding is a new industry. It is hardly older than ten years. But it has developed at once on a commercial scale. Experience proves it to be highly profitable, and the conviction is rapidly spreading that no corn grower can afford to be ignorant of its principles and its results.

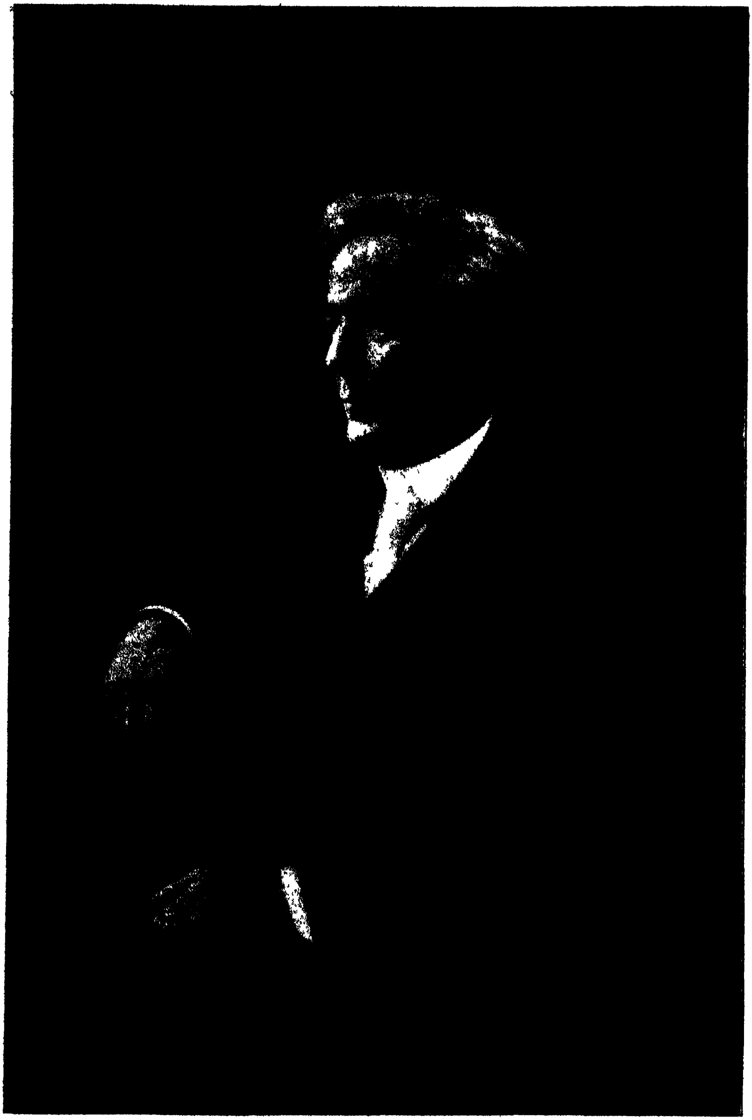


Fig. 49. Luther Burbank of Santa Rosa, Cal.

IV

THE PRODUCTION OF HORTICULTURAL NOVELTIES BY LUTHER BURBANK

A. METHODS AND MATERIAL

The commercial catalogues of the horticulturists contain, yearly, a certain number of novelties. Some of these are introduced from foreign countries, others are due to accidental sports, but many are the results of artificial improvements. They are produced either by nurserymen or by private persons who charge the seedsmen with their sale. As a rule, this production of novelties is a subordinate matter. It is very rare to find a man who devotes his whole life and all his energies to the introduction and production of new, beautiful or useful, horticultural plants.

Such a man is Luther Burbank of Santa Rosa in California. He is a nurseryman, but has no nursery in the ordinary sense of the word. He is a tradesman, but sells nothing besides his novelties, and these only to other dealers who will multiply them and offer them to the general public. His aim is not the accumulation of wealth, but to contribute to the welfare of other men by giving them better food, better fruits, and more beautiful flowers. He is especially interested in the production of cheap ornamental plants for private gardens, in order to disperse their enjoyment as widely as possible. He is not engaged in pure scientific research, but of late he has consented to have his methods and cultures published, that they may become a guide for other men in their work along the same line. The Carnegie Institution of Washington has accorded him an annual grant of $10,000 for ten years, thus enabling him to extend his cultures on as large a scale as is possible for the work of one man. More-

over, the Institution will take in hand the recording of the history of his experiments and thus create a source of practical and scientific information of the highest importance upon many questions of plant-breeding.

Such a standard work is the more needed, since the methods and results of European horticulturists, are, as a rule, accessible to American breeders only with difficulty. Burbank has had to rediscover many of the rules and practices which in Europe were more or less universally known. His science and methods are his own work, although in comparison with those of other horticulturists they do not contain essentially different procedures. It is a most interesting study to go into the details of such a comparison, especially since, by the same principles, he has obtained such striking new results. If his work does not enlarge our knowledge of the general rules, as it is not intended to do, it, at least, provides us with such numerous illustrations that a description of his experiments, even if but brief and incomplete, may be considered as a review of almost the whole field of horticultural plant-breeding.

From this point of view I shall now give a survey of Burbank's work. In doing so it is not my aim to recommend his fruits or his flowers. They recommend themselves, and their world-wide appreciation gives the best proof of their high value. I am concerned only with the methodological side of the work, and my main aim is to describe such details as will best contribute to the establishment of the full agreement of Burbank's experience with the agricultural methods of Nilsson on the one side, and with the latest results of biological investigation on the other.

Luther Burbank was born March 7, 1849, in Lancaster, Mass. His father was of English and his mother of Scottish ancestry. He was reared on a New England farm and indulged in the breeding of American grapes and of new

Fig. 50. Burbank's farm at Santa Rosa, Cal., showing the residence, the greenhouse, the shed, and part of the experiment garden. Photograph of the S. Pac. R. R. Co.

potatoes, which was quite a common pursuit in Massachusetts about the year 1873. He succeeded in raising some new varieties of potatoes in that year, multiplied them during two succeeding summers and offered them for sale to the well known seedsmen, Messrs. J. J. H. Gregory & Son at Marblehead, Mass. They selected one variety among the three he had offered and paid him $125 for it. This happened in the summer of 1875, and in September of the same year, Burbank left Massachusetts and settled at Santa Rosa, California, partly on account of his health, partly on account of the bright prospects which the climate of that part of California offered him for his most beloved occupation, the improvement of plants. For at Santa Rosa almost all the garden plants, which require greenhouses in the eastern states, can be cultivated in the open, and therefore on a much larger, or even on an almost unlimited scale. As an instance, I mention the Amaryllis.

In the beginning, Burbank rented a small nursery near Santa Rosa, and cultivated market flowers and small fruits, but had to look for work on other farms also, in order to gain money enough for maintenance. It was only after 13 years, in 1888, that he had saved enough to buy his present farm. Here he organized a large nursery and soon accumulated a small capital, which enabled him to sell out his business, in the year 1890, and to devote his whole life to the introduction and production of novelties. Three years afterward (1893) he published his first catalogue on "New Creations in Fruits and Flowers," which gained for him a world-wide reputation and brought him into connection with almost all the larger horticultural firms of the whole earth.

In 1905 he accepted the Carnegie grant and was appointed an honorary lecturer on plant-breeding at the Leland Stanford Junior University. Here he delivers two lectures a

Fig. 51. Experimental garden of Luther Burbank at Santa Rosa. A spineless cactus is seen along the fence. Cultures of Echeveria and other species in t e foreground Photograph of the S. Pac. R. R. Co.

year before a score of advanced students and professors, illustrating his new creations by means of specimens and photographs, and explaining the experiments by which they were won.

In the meantime, the potato which he sold to Messrs. Gregory had proved to be a great success. It had rapidly increased in importance and supplanted many of the older cultures. According to an official statement of the United States Department of Agriculture at Washington made a few years ago, this Burbank potato is adding to the agricultural productivity of the country an annual amount of $17,000,000. In the eastern states it is cultivated alongside other varieties and is often indicated by local names instead of Burbank's name. But along the Pacific Coast. from Alaska to Mexico, it is now the standard of excellence among potatoes. In fact, it is almost the only variety cultivated in California, where the culture of potatoes for cattle feeding or for factories is of hardly any importance. Its tubers are of a large and (what is more important) almost uniform size.

The evidence which is set forth in this discussion, I gathered mainly during my visits to the Santa Rosa and Sebastopol farms of Burbank, where he was so kind as to explain his cultures to me and to answer all my questions about them. I visited him twice during the summer of 1904, and had the privilege of a four-days' intercourse with him in July, 1906. Of course, I had prepared myself for these visits by studying the magazine articles on his work published during the last few years, and among which those of E. J. Wickson in Sunset Magazine may be cited as the most complete and the most reliable. Wherever possible, however, I submitted the statements once more to my host, asking him such questions about them as would meet the doubts which might offer themselves from the standpoint

Fig. 52. Luther Burbank in the garden before his house at Santa Rosa, Cal., receiving a visit of the author of these essays (in the middle), and of Dr. G. H. Shull of the Carnegie Institution (to the right).

of a biologist. As a rule, the answers covered my wishes and led to the conclusion that notwithstanding the widely divergent, and on some points quite opposite, methods the main results of practice and science are the same.

In order to understand the kind of evidence which will be discussed here, it is necessary to have a clear idea of what a visitor can see on the farms. As soon as Mr. Burbank has originated a new kind of useful or ornamental tree, flower, fruit, or vegetable, he sells it to one of the great seedsmen, florists, and nurserymen with whom he is in constant relationship. They take the whole stock, multiply it and offer it to the trade. They buy the exclusive right of selling the new variety, and nothing of it is left on the farms of Burbank. Hence it follows that a visitor cannot expect to have a survey of the achievements that have already been made. There is no collection of these in living condition. One may study the commercial catalogues of Burbank or inspect his numerous photographs, but the perfected varieties themselves are no longer there.

On the other hand, the visitor to the experiment-farms will become acquainted with the novelties destined for the immediate future. Burbank will explain to him his aim and his hopes as well as the methods by which he expects to fulfil them. The future, however, is uncertain, and the real value of a novelty can be judged only after some years have elapsed after its introduction into general culture. The spineless cactus opens the brightest prospects for the cultivation of the arid deserts, but the trial to determine whether it will succeed under those unfavorable conditions and will reward the expenses of its cultivation must still be made. So it is in many other cases too. Burbank himself is the most exacting judge of his productions and insists that they shall stand all tests of culture and trade and shall survive such exacting trial or perish.

From this discussion it may easily be seen that my evidence relies, for a large part, on experiments which are not yet finished and the ultimate result of which cannot yet be estimated. For the description of the methods used, this is of no importance, and in many cases the older experiments with their practical results will have to be alluded to.

Burbank's first catalogue was published in 1893. It is now 13 years old. The varieties described therein are, of course, older, but they are only a small number in comparison with his present stock. The larger part of his experiments are younger, and only a few of his pedigrees cover more than ten years, as, for instance, those of the plums.

A special feature of Burbank's work is the large scale on which his selections are made. It is evident that in a variety of mixed condition, or in the offspring of a hybrid, and even in ordinary fluctuating variability the chance of finding some widely divergent individual increases with the number of the plants. In some hundred specimens a valuable sport can hardly be expected, but among many thousands it may well occur. The result depends largely upon these great numbers. In one year he burned up sixty-five thousand two and three year old hybrid seedling berry bushes in one great bonfire, and had fourteen others of similar size. He grafts his hybrid plums by the hundreds on the same old tree, and has hundreds of such trees, each covered with the most astonishing variety of foliage and fruit. Smaller species he sows in seed-boxes and selects them before they are planted out, saving, perhaps, only one in thousands or ten thousands of seedlings. Thornless brambles, spineless cacti, improved sweet grasses (Anthoxanthum odoratum), and many others I saw in their wooden seed-boxes being selected in this way.

The same principle prevails in the selection of the species which are submitted to his treatment. Here, also, the result depends chiefly upon the numbers. He tries all kinds of

berries and numerous species of flowering plants. Some of them soon prove to be promising and are chosen, others offer no prospects and are rejected. The total number of the species he has taken into his cultures amounts to 2,500. The list of the introductions of last year shows 500 species, mostly from South America and Australia. Formerly he often made excursions, in order to collect the most beautiful wild flowers or the best berries of Northern California, but for several years he has had no time to spare for this work. He has two collectors, who collect only for him, and many correspondents who send valuable bulbs and seeds, from time to time. One of his collectors travels in Chile, the other in Australia, preferring the regions in which the climate corresponds best with that of Santa Rosa. The Australian plants are usually sent to him under their botanical names, the South American often without any names at all, only the date and locality of collection being indicated. This insufficiency of denomination is of no importance at all for the practical work, but often diminishes the scientific value of the experiment, as for example, in the case of the spineless cactus. The thornless species with which he crossed the edible varieties have been sent to him from Mexico and elsewhere without names, and they have been eliminated from the cultures as soon as the required crosses have been made. Hence it is evident that a scientific pedigree of his now renowned spineless and edible cactus will always remain surrounded with doubt as to the initial ancestry.

Besides his collectors in other countries and his correspondents widely scattered through the United States, he is constantly on the lookout for odd sorts of fruits or flowers, in order to combine them with the existing varieties. He procures seeds from the nurseries of all countries, from Europe and Japan as well as from America. He brings together, in each genus, as many species as possible before

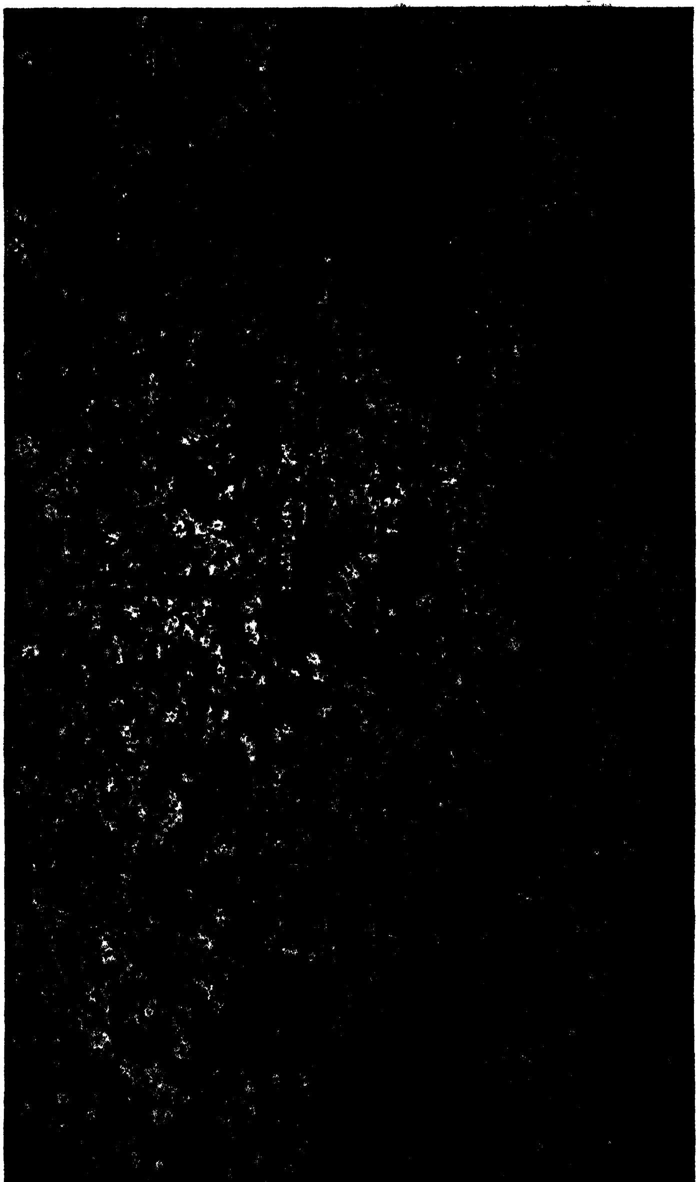


Fig. 53. A field of improved Australian Star-Flowers on Burbank's home farm.

starting his crosses. Of Asclepias I noted about 20 species on a plot, of Brodiæa four, of Rhodanthe, Schizanthus, and the fragrant Tobacco all the best and newest European varieties and hybrids. Many other instances will be given in the special descriptions. Among grasses he is now trying species of Lolium, Stipa, Agrostis, and Anthoxanthum, partly for forage and partly for lawns. Of evening primroses he had received a large flowered form of the creeping white Œnothera albicaulis, which he has now selected along with other small and large flowered yellow primroses. Many wild species afford deviations, which are ordinarily considered as monstrosities, but which in his hand may be improved to yield valuable ornamental plants. He showed me a beautiful yellow papaveraceous plant, the Hunnemannia fumariæfolia from Mexico, which in some specimens doubled its flowers on the outside instead of within, in the same way as some Gloxinias. Many other introduced deviations and hundreds of beautiful species I saw, but there is no reason for mentioning their names here. Very often a wild strain supplies some valuable quality or perhaps only the vigor of growth which fails in its cultivated allies. Many a weak race was made strong by this means.

Among the species and varieties introduced from foreign countries some proved to surpass the corresponding American forms without needing any improvement. In this way very valuable contributions to American fruit culture have been secured. In the beginning of his work, a Japanese agent one day sent him some plum pits. From these he grew two varieties, which he has since introduced under the names of Burbank and Satsuma plums. The first of them was named for him by the United States pomologist at Washington. It was exceptionally suitable to American conditions and has justified its selection by its present wide distribution and economic value. The Satsuma plum is now commonly

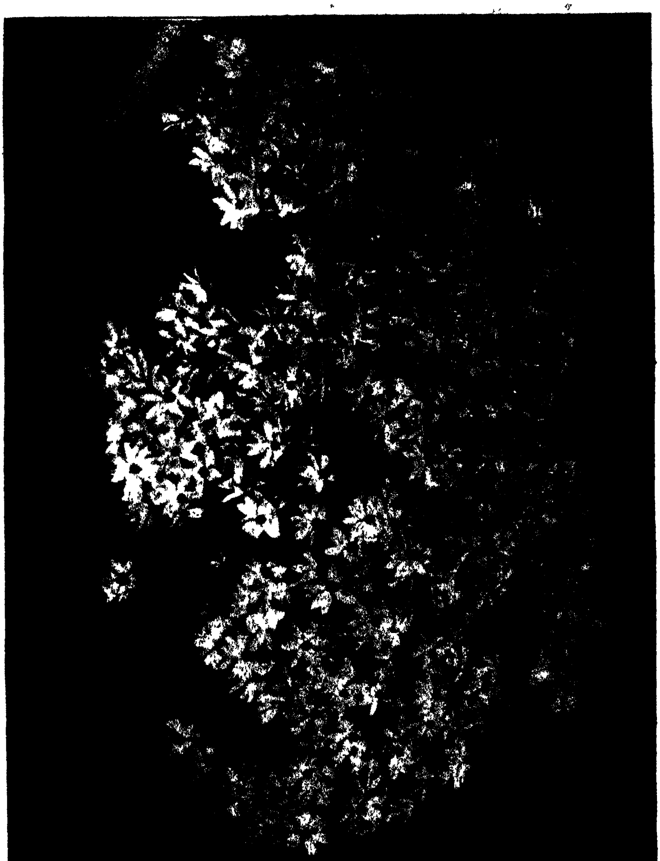


Fig. 54. The improved everlasting Australian Star-Flowers.

cultivated in California and is a most delicious preserve on account of its sweet flesh and small pits. The Burbank plum, on the other hand, is one of the best and most popular Japanese plums throughout all the United States, it is early and heavy bearing, free from insects and diseases, and a market fruit of large size and attractive color.

Other species needed only sowing on a large scale and a selection of the best individuals, and could then be introduced without artificial improvement. The common French prune, of which California has produced one hundred and fifty millions pounds of dried produce in a year, is a small fruit and late in ripening, although it is rich in sugar. In order to enlarge the size and to change the time of ripening, Burbank sowed large numbers of seeds of this French prune d'Agen, grafted the seedlings on older trees in order to force them to yield their fruits soon, and finally chose among the thousands of grafts the type which is now known as the sugar prunes, a large fruit ripening a month earlier and prolific in bearing. In the same way, the crimson rhubarb, or mammoth pie plant, was secured which is now grown on a large scale all around Los Angeles, whence it is shipped, during the winter months, to the markets of New York. It is a continuous bearer throughout a large part of the year and has a peculiarly delicate flavor. It was sent to Santa Rosa by Messrs. D. Hay and son, nurserymen in Auckland, New Zealand, about fourteen years ago. Burbank sowed the seeds on a large scale, and selected the best type for introduction as soon as he perceived its excellent qualities. Among flowers, the Australian star flower or everlasting (Cephalipterum Drummondii) is now being introduced after only a few years of multiplication and selection. It is a composite, and its apparent flowers are, in reality, flower heads, the bright red color of which is due to the bracts of their involucres, as in other species of everlastings. It is

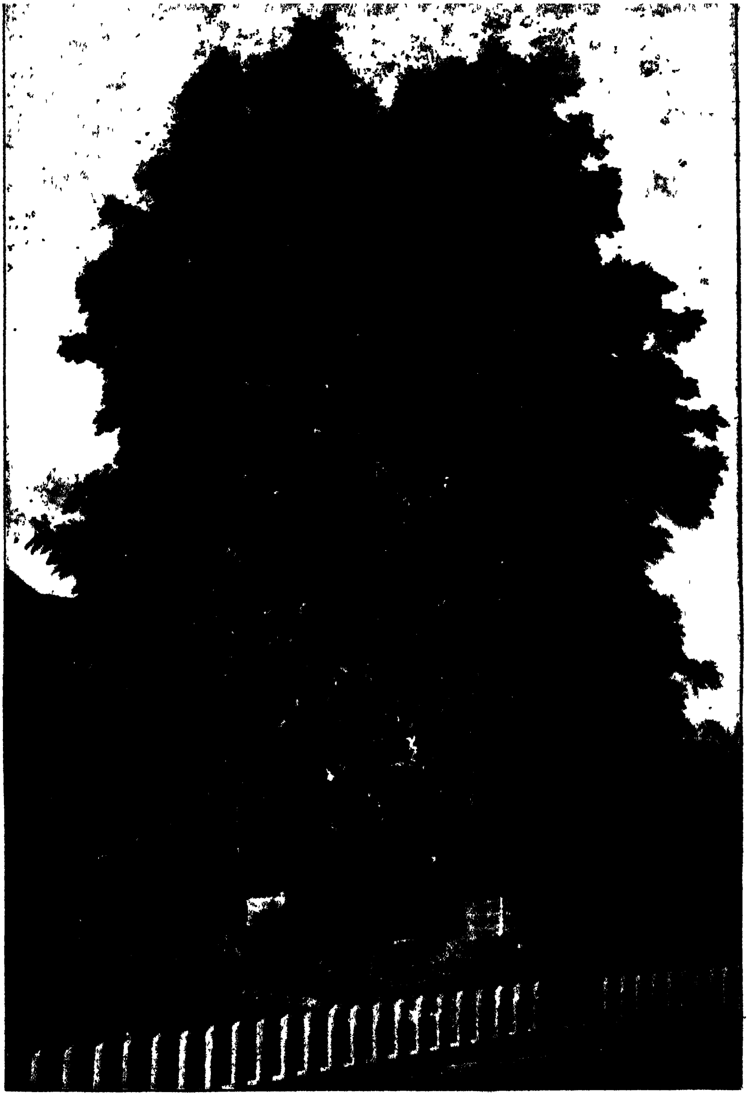


Fig. 55. A hybrid walnut (*Juglans Californica nigra*), reaching double the height of ordinary trees.

recommended for millinery purposes and may supplant a large part of the trade in artificial flowers. I admired, on each of my three visits, the large beds full of the shiny red flowers, and saw the selection of the largest and brightest specimens going on.

The main work of Burbank, however, consists in producing new varieties by crossing. The aim of crossing is the combination of the desirable qualities of two or more species and varieties into one strain, and the elimination of the undesirable characters. In the most simple cases this can be produced by one cross and without selection; but, ordinarily, many crosses and the production of a more or less chaotic progeny are required, and selection has to decide what is to live and what is to be rejected. It is a well known fact, discovered by Koelreuter and Gärtner and confirmed by numerous other scientific hybridologists, that hybrids often surpass both their parents in the vigor of their growth and the profuseness of their flowering. Taking advantage of this rule, in more than one instance Burbank has produced hybrids of extreme capacities. The most astonishing instances are afforded by his hybrid walnuts. In the year 1891, he crossed the English walnut and the Californian black walnut and afterward planted a row of them along the road before his residence. At the time of my first visit, six gigantic trees were seen growing. They had reached twice the height and size of ordinary walnut trees. Three of them he has since been compelled to cut down, because they increased too rapidly. This summer (1906) I saw the three remaining specimens, 80 feet in height and 2 feet in diameter. He showed me sections of the cut stems. Their wood was of a fine grain, very compact and of silky appearance. The annual layers measured about 5 cm., a most extraordinary thickness. Fast growing trees are usually of soft grain, but these hybrid walnuts have a wood as hard as that of the

ordinary species. By recrossing them the qualities of the wood have been still further improved, and selection in this direction produces a broad variety of hard and soft, coarse and fine, plain and beautifully marked, straight and wavy grain. In driving me to his Sebastopol farm, he pointed out an enormous walnut tree in one of the gardens along the road. It far surpassed all the surrounding trees, though many of them were older in age. It is a hybrid between the native California black walnut and the New England black walnut. It is, next to the redwood and big trees, perhaps, the largest tree and the fastest grower I ever saw.

Another tree which displays the vigor of hybrids is the Wickson plum. It is a little more than ten years since Burbank distributed the first grafts of this variety, and it was the first of his plums to make a deep impression on Californian fruit growers. It was produced by crossing the above named Burbank plum with the Kelsey, both parents being varieties of

Fig. 56. Extreme variability in the size of seedlings of hybrid walnuts in the second generation.

the Japanese Prunus triflora. The flesh of the Burbank is red, that of the Kelsey being dull pink and green. The special merit of the breeder lies in the choice of the parents from which to produce his hybrid. The Wickson plum is, at present, most largely grown in California for shipping purposes on account of its high durability. It has the unique heart shape of the Kelsey, but the flesh of the Burbank, a rich garnet and yellow color, a large size, and a perfect shape. It is very juicy and delicious, but its firm skin insures good shipping and keeping qualities. Its first sales in Chicago made the record for plum prices in the United States. It is widely distributed over the world, though somewhat less hardy than other varieties. It has the best qualities of both parents and in many respects surpasses both of them. It is one of the best illustrations of what can be obtained in a single crossing by a man who thoroughly knows all the qualities and characters of his trees and how to combine them, and who is guided by this knowledge in the choice of the parents for his cross.

It is exceedingly difficult to gain a correct idea of the influence which the introduction of such novelties can have over the horticulture of some definite country or state. The Burbank, Satsuma, Sugar, and Wickson plums are now largely cultivated in California as well as elsewhere. They have partially supplanted old varieties and have, also, been the means of increasing the acreage devoted to plum culture. But it is manifest that the change of varieties requires the regrafting of the orchards and cannot be performed at once. It often requires ten years or more to revolutionize an established and profitable industry on any large scale. It takes some years to prove the trustworthiness of the new sorts and to convince the fruit-growers of the desirability of the change. The production of a new variety is one great step, but its introduction and distribution is another equally

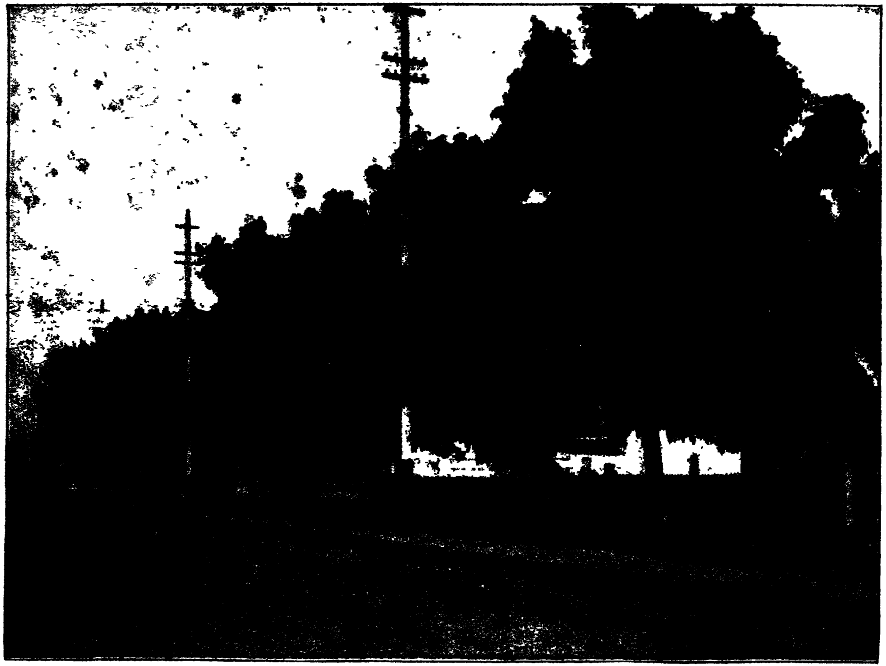


Fig. 57. A row of hybrid walnuts before the residence of Luther Burbank at Santa Rosa.
Photograph of the S. Pac. R. R. Co.

important one. The whole fruit-growing industry of California amounts to an aggregate value of about sixty millions of dollars annually, and of this sum hardly one per cent is represented by the varieties imported or created by Burbank. If we compare these figures with those given foi the importance of the Burbank potato, we find a great difference. But for a fair appreciation we must realize that the Wickson plum is scarcely older than the ten years required for its first wide distribution and that most of the other hybrids created by Burbank are much younger. We must leave it to the future to decide what will be the real significance of the improvements in fruits and flowers, of which this one man has produced such an astonishing number of excellences.

B. NEW VARIETIES OF FRUITS AND FLOWERS

Since the time of Darwin, the methods and achievements of the breeders have played a large part among the arguments adduced for the support of the doctrine of evolution. In a broad sense they give us an insight into the processes by which new forms are originated, and since the general laws of variability must be the same for the cultivated condition and for the phenomena of nature at large, there can be no doubt about the general validity of the argument. The experience of the breeders teaches that new forms from time to time arise from the existing ones. It gives a general idea concerning the affinity of the parent types to their offspring, showing the similarity to be very large and the produced differences correspondingly small. On the other hand it shows that by the accumulation of small differences, wider divergences may be obtained. This evidence led Darwin to one of the main propositions of his theory of evolution, viz., that the larger groups in the vegetable kingdom have originated in the same way in which the smaller types are still seen

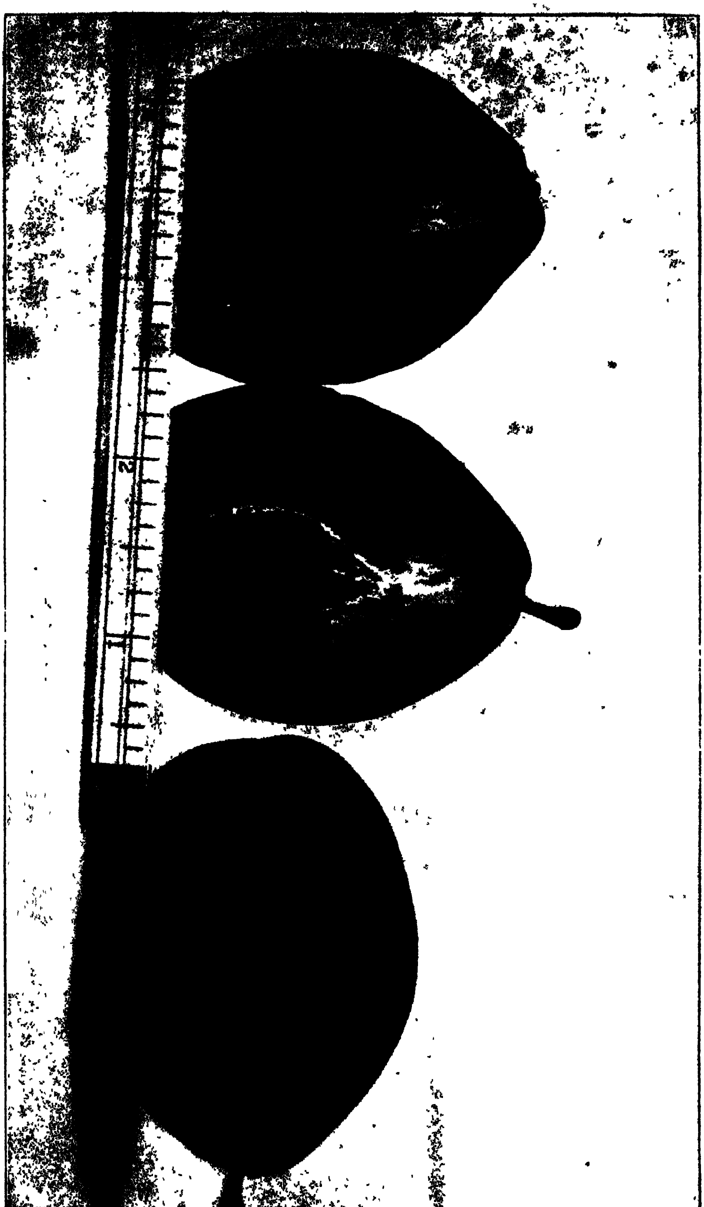


Fig. 58. Burbank Giant prune.

to come into existence. This proposition can be proved, and in fact has been proved, independently of the question concerning the details of that origin.

This broad principle of evolution by means of natural laws having been established, the question naturally arose, how far the breeder's experience could be considered as a reliable guide in evolutionary problems. On this point, however, many difficulties have arisen, all owing to the simple fact that practical breeding and scientific experimenting are things of altogether different purpose and method. Of late it has been contended that the discussion of the scientific side of the question should abstain from the use of the breeders' results. There can be no doubt that in the end this will prove the right way, since only then it will be possible to submit all arguments to the most severe criticism.

At present, however, the purely scientific investigations concerning variability and inheritance are only in their beginning. Some fields have been more or less thoroughly explored, and definite laws have been discovered. But the more complicated cases are as yet hardly accessible to our analysis, and the breeders' experience often covers so long a series of years that the science of evolution is still quite inadequate to be compared with it. Moreover, the practical results contain so many indications and hints for the starting of investigations, and so many details which otherwise could easily be overlooked, that they are still contributing a most valuable support to evolutionary science.

In estimating the value and reliability of the breeders' work for theoretical discussions, its methods and aims should clearly be understood. The practical work chiefly consists in the selection of those specimens which are most suitable for the purpose under consideration. But selection requires material to choose from. This material, in some rare instances, may be directly afforded by nature, but in the larger

Fig. 59. Burbank Sugar prune.

number of cases, it must be procured artificially. The production and augmentation of variability is therefore to be considered as a second point of almost equal importance to the selection itself. It may be either plain and simple or intricate. In the simple cases it is often possible to trace the whole line of the work which has led to the ultimate result. In the more intricate cases, however, the breeders' purpose is simply to increase the material for their selection as largely as possible. All means conducive to this are combined and the scientist finds himself at a loss in trying to discern the real causes from amidst the chaos.

For this reason, I shall limit my present discussion to the more clear and simple instances, leaving the complex cases for my next chapter. Of course, a sharp limit cannot be expected, and an arbitrary choice is unavoidable.

The investigations of the past decades have led to the recognition of various kinds of variability, and all further research has to start from these distinctions. The breeders, on the other hand, are not concerned with these divisions and simply consider the variability of their plants as such. But variability embraces on one side the existence of a larger or lesser range of different types, and on the other hand the actual transformation of one form into another. It is evident that a scientist wishes to know in each case to which of these two types an observed fact of variability belongs, while this distinction may be indifferent to the practical man. In some cases, however, it is not at all indifferent. I mean those improvements which have to produce races that can be multiplied by seed. All the varieties of cereals, most of the other agricultural crops, and many kinds of garden plants belong to this group. Here it is manifest that only inheritable variations are of consequence, or strictly speaking, only those that will be repeated by generations raised from seeds.

If, however, a new type is not intended to be reproduced

by seed, the available range of variability is much larger. Such is, among the larger crops, the case of potatoes. Moreover it is the rule for fruit trees, which are multiplied by budding and grafting, and for all the garden plants which are reproduced from bulbs, roots, layers, or cuttings. In these cases, inheritance by seed has manifestly no significance at all, and all kinds of variations, which would disappear or be more or less reduced after sowing, here have the same value as the strictly inheritable characters.

In other words, the range of variations is widened if the selection is limited to varieties with vegetative propagation, and restricted when seed varieties have to be produced. It is difficult to give an idea of the extent of this difference, but it may be stated here that the best estimates lead to the assertion that for vegetative varieties selection finds a field thrice as large as for seed varieties. Correspondingly, the ameliorations may be thrice as important and productive in the former case as in the latter. Hence it is evident that whenever a species can advantageously be multiplied in the vegetative way, its artificial varieties will manifestly excel those of ordinary seed plants.

The most simple case of producing new varieties is to make use of ordinary fluctuating variability. By sowing on a large scale, the extremes of this variability will easily be obtained, and they will surpass the average the more, the larger the number of seedlings examined. One or two of the best individuals are chosen and the rest destroyed. The chosen samples then become the origin of a new variety which will remain constant as long as it is propagated only in the vegetative way. As a first instance, I choose the loquat or Japanese quince (Eryobothrya japonica). This species has small yellow fruit of an acid taste, almost filled with the large seed, which is covered with only a thin layer of fruit flesh. But it has a peculiar flavor found in no other fruit.

Of this species, Burbank has sown thousands of seeds and cultivated the seedlings until they ripened their first fruits. Among them he has chosen one excellent individual, which is still growing on his farm near Sebastopol. It is a tree about six feet high, with wide-spreading fruit-laden branches. Its quinces have the same aroma as the ordinary loquat but are much larger and of an orange yellow color. Their seeds are not larger than those of the ordinary species, but the juicy fruit flesh is greatly developed in thickness and very delicious. These new Japanese quinces are considered as a notable improvement, making one of the finest delicacies for the table. In the same way, Burbank is trying to improve the California currant (Ribes sanguineum). This species is also known as the flowering currant of the Pacific coast and is popular in European gardens as an ornamental spring-flowering shrub. It flowers profusely but is poor in the ripening of its fruits. In California it is abundantly found in the wild state, and is often densely covered with racemes of small blue berries. It occurs in quite a number of elementary types, slightly differing according to their localities. Those of the northern districts along the Pacific coast are notably hardier in winter than the more southern varieties. In such cases, selection has to begin with the choice of one or two of the elementary species, and Burbank preferred the hardiest, which he secured from British Columbia. In sowing the seed of this variety on a large scale, variations in the size and color of the blossoms, in the number of flowers on the raceme, and especially in the development of the fruit, soon appeared. Among those he chose the best plants in different directions, some having long clusters of bright blossoms, others distinguished by an increase of the pulp of the berries or an improvement in the flavor. Long rows of shrubs with an almost inconceivable variety of fruits may now be seen on his farm. Among these a definite choice must still be made and proba-

bly more than one variety will recommend itself sufficiently for introduction into the market. Thus a new kind of currant with a higher and more specific aroma will be added to the already existing varieties. It is, however, Burbank's purpose to submit these new selections to the process of hybridization by crossing them with some other indigenous types, as, for example, the glutinous variety found wild in the region of San Francisco (Ribes sanguineum glutinosum).

Another wild California fruit recommends itself for improvement. It is the Elæagnus, the pale yellow berries of which are produced in such large numbers that the branches are often seen bending under their weight. They are juicy enough, but the taste is not that which is required to make it a palatable fruit. Burbank has selected quite a number of types and sown them on a large scale in order to gain a marketable berry. By cultivation the plants have lost their thorns, as in other instances, and the shape and vigor of the whole shrub is notably improved. An increase in fertility and some amelioration of the taste has also already been obtained, but a large number of highly variable plants are still awaiting ultimate selection.

Freeing brambles of their thorns may seem to be an arduous problem, but reducing the thorns to practical harmlessness is not at all difficult, for the prickles are variable in number and size like any other character, and among many thousands of plants some will be found very rich but others very poor in these appendages. This character has the great advantage of showing itself in early youth, and so the choice may be made from among the young plants when still in the seedling boxes. All the prickly ones are rejected, and only the smooth ones planted out. It is an astonishing sight to see those long rows of harmless brambles awaiting further selection at the time they ripen their berries.

The adduced instances may suffice to illustrate the prin-

ciple of selection resting simply on the ground of ordinary or fluctuating variability. Its possibilities, however, are limited, and since the breeder is always on the lookout to widen the range of his material, it is but seldom that he is content with this process of pure selection. In almost all cases, he will try to increase the elements of his choice, and in order to do this, he takes to the process of hybridization.

Hybridization, however, is not always a means of increasing variability. In some instances hybrids are as constant and uniform as their parent species even when propagated from seed. A certain number of wild types formerly considered and described as pure species have since been proved to be of hybrid origin, the types having been artificially produced by repeating the assumed original cross. Kerner von Marilaun has described quite a number of such instances, and Janczewsky and others have produced hybrids which cannot be distinguished from real species otherwise than by the historical record of their birth. In such cases the breeder has to be content if his hybrid proves to excel its parent species in some industrial quality, but without renewed crosses his work is limited to its production and propagation.

Some such cases have occurred in Burbank's work also. As an instance I will adduce the case of a bramble. A cross has been made between the wild Californian dewberry (Rubus Californicus) and the Siberian raspberry, or Rubus Sibiricus. The first is a small species of bramble and the second closely allied to the common raspberry. But in both the fruits are small and worthless. The hybrid, however, surpasses both its parents in this important respect, having large black berries, which are produced abundantly and ripen several weeks earlier than both parents. As the first notable improvement among brambles, it received the name of primus-berry. Under this it has found its way into the market. Other constant hybrids have since been pro-

duced in the same genus, among them the phenomenal berry, which may be described as a gigantic red raspberry, and which is now the most noted. It is a hybrid between the Californian wild dewberry and the Cuthbert raspberry. All of them may be reproduced from seed as well as in the ordinary vegetative way.

The increase of variability which commonly is the aim of hybridization may be induced along definite or indefinite lines. In other words, the combination of characters which is the chief aim of crossing, may be so simple as to be easily calculated beforehand, or it may be so intricate as to produce a chaos of forms among which selection will ultimately become the real factor of improvement. For scientific purposes, the more simple cases are in many respects the most interesting, and for this reason we shall now proceed to the discussion of some of them.

It is a much discussed question whether new characters may be produced by crossing. Of course, there is no doubt that new varieties and new races may originate in this way, but this is not the same point. It is well known that the larger number of hybrids simply owe their character to a new combination of qualities. It is the combination which is new, not the qualities themselves. Some characters are derived from one parent, others from the other. Each of them may simply be inherited in the same way as in the case of pure descent. But by their new combinations they yield varieties of higher practical value, and notable examples are afforded in those cases where one parent has contributed vigor of growth, hardiness in winter, resistance to disease, or productivity, and the other bright flowers, palatable fruit, or nutritious seeds. For the breeder, such combinations of characters have, of course, the same value as single favorable marks, but from a biological point of view the two principles must be sharply distinguished. The combination of

characters produces nothing really new, and since this is the ordinary case in horticultural crossing, the question naturally arises whether, besides them, from time to time, new elementary characters may arise by hybridization.

Burbank's experiments contain a number of cases in which the appearance of actual novelty is quite striking. Therefore I have discussed this question with him fully, and the result is the conviction that the novelties in question are only apparent, and that the real work of the breeder is not the casual or accidental production of such, but a systematic search for rare and as yet unnoticed, or perhaps, even forgotten qualities. It is based on his power to appreciate the industrial value of characters which formerly had been simply overlooked or considered of no promise in a commercial direction.

Before considering Burbank's results in this line of facts, a few other illustrative examples may be adduced. One or two decades ago, a considerable number of varieties of double-flowered lilacs had been produced by Lemoine at Nancy, France. All of them were hybrids, and as such were very ornamental shrubs, with large clusters of bright flowers, which excelled the older kinds by flowering during a noticeably longer time. The double flowers, however, were no result of the crossing but had been introduced as such into the group of the ordinary varieties, by crossing them with an old and forgotten double-flowered form, which of itself was hardly ornamental on account of its small flowers. It was the Syringa azurea plena, and the real source of Lemoine's enormous success in this case was his idea of buying a tree of this variety and of starting a series of crosses with it.

Another instance is the seedless apple, which is now being introduced into the trade as young grafted trees, which are expected to exercise large influence on the whole culture of

apples as soon as they are full grown, and shall have been put upon the market. The character is nothing new. It occurs in different varieties of apples and even of pears, but it seems to have always been combined with some defect which made the varieties useless, or at least, of inferior quality. Nobody seems to have suggested the idea of combining with this quality the character of our best varieties, and so our apples and pears are still in possession of the cores and their seeds. What is new and promising for this most important industry is the combination of this rare and almost forgotten character with the qualities of a good and marketable fruit.

One of the most interesting instances of this kind of work on Burbank's farms is the white blackberry, a hybrid race with abundant clusters of most delicious fruit of a perfect white. How can such a simple mark as the lack of the black color evidently is, be produced by crossing? The answer is very simple. Even as in Europe a white variety of the raspberry from time to time occurs, so there is found in the eastern states, among the cultivated brambles, an insignificant variety with small pale berries. As soon as Burbank had discovered this fact, he secured some of these pale yellow berries, introduced the type into his culture, and crossed it with the variety called Lawton's blackberry. The result was the combination of the white color with the excellent qualities of the other parent. In a similar way, notable qualities of rare or wild species have often been transferred by crossing on cultivated varieties, thus giving rise to whole groups of races of a new stamp.

Another instance is the stoneless prune, one of the most celebrated marvels of the Sebastopol farm. Only one of its varieties is ready for the trade, but the remainder are still in a period of crossing and selection. A prolonged treatment must still give them the same size, fleshiness, and flavor as

other prunes have. The fruits we saw were of a clear blue color and very attractive, though yet small. One may bite completely through the middle of the prune, no stone being met with. Inside of the plum is the seed, like an almond in its shell, and with a fine taste like that of an almond, but without any hard covering. It is surrounded only by a pale jelly with some stray remnants of hard stony material, which do not offer any resistance to the teeth or to the knife.

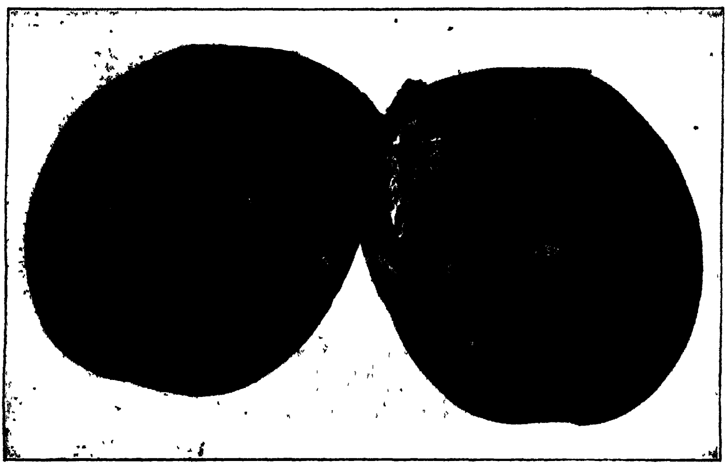


Fig. 60. The improved stoneless prune. The pit is not surrounded by any stony material, but by a jelly.

All around the jelly is the clear, greenish, and juicy fruit flesh, exactly as in an ordinary plum. The amount of stony remnants varies greatly along with the other characters. Some hybrids are more stony, others less. The latter will be chosen, in order to be crossed with large, highly flavored prunes, so as to obtain a superior quality, or they may be crossed with all other existing cultivated varieties in order to transmit the lack of a stone to all of them, and so ultimately to replace all the present varieties by correspond-

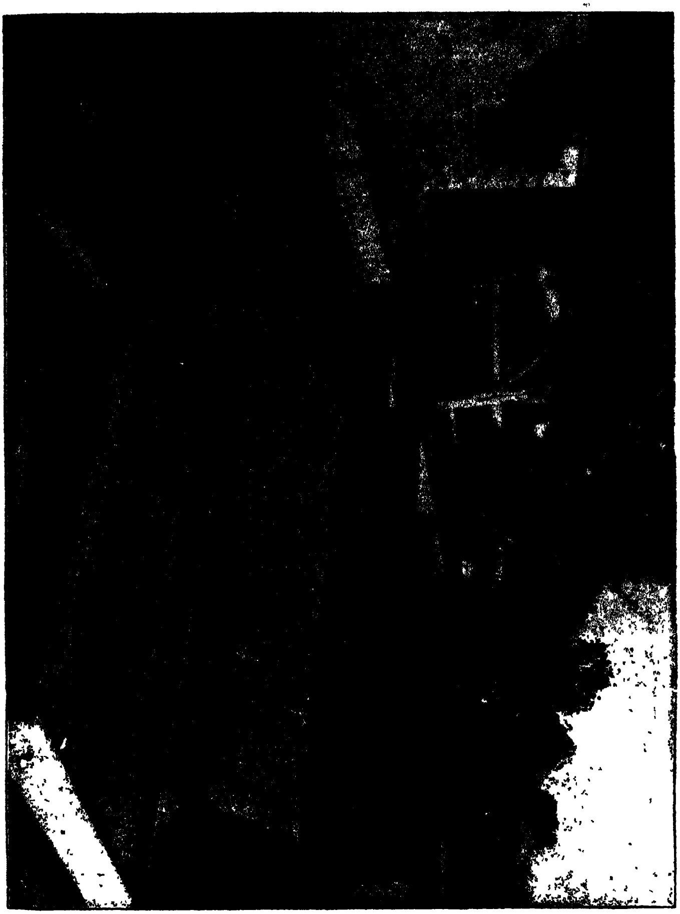


Fig 61. Hybrid Cactus Seedlings at Santa Rosa, 1904

ing stoneless ones, each of which will be appropriate for the the same culture and use as one of the older types. Here, once more, the question arose, can the disappearance of the stone be the result of the hybridization of two or more ordinary varieties? Burbank's answer was a negative. He had followed quite another way in procuring this astonishing result. He had noted that about two centuries ago, in France, a prune bore the name of "Prune sans noyau." It was an indifferent variety, more a curiosity than a thing of commercial value, since it produced only small fruit. But Burbank at once realized all the possibilities which this stoneless form offered. He was quite convinced that it needed only to be crossed with the best ordinary kinds to give a new and most attractive fruit. He procured seed of this long-forgotten French prototype and sowed them on his farm. By their first fruits he satisfied himself of the correctness of the description of them, and of their fitness for his work. Of course, by one crossing, the chance is not large enough to get a desirable combination. Repeated crossings are required, and each has to be accompanied by a selection of the most promising specimens. In this way, size, flavor, and fleshiness may steadily increase, while the amount of the remnants of the stone is always kept as small as possible.

A counterpart to the stoneless prune, is the spineless cactus. It belongs to the genus Opuntia, some species of which are very celebrated, since they produce the Indian figs, which may be seen in the markets of New York and elsewhere in the eastern states, where, notwithstanding their spines, they are highly appreciated as a delicacy. The Opuntias are desert plants, growing abundantly and in quite a number of species on the plains of the semi-arid regions of the West. Their stems consist of large flat pods, joined together in the most fantastic manner. They are often seen

Fig. 62. The Spineless Edible Cactus, a hybrid between the wild spineless species and the cultivated varieties, growing along the fence of Burbank's farm at Santa Rosa.

reaching a height of some six feet, with numerous wide-spread branches. Their fruit is relished by cattle, being juicy and nutritious, and not too spiny. The disc-like segments of the stem also contain nutritious food, and this is sometimes made use of, the prickles being softened by cooking under the influence of the juice from the cellular tissues. But cooking is an expensive mode of preparation, and thus the thorns prevent the use and culture of the cacti on any large scale.

From this discussion it is evident that a spineless edible Opuntia would be a most welcome addition to the agriculture of the semi-arid West. It could be cultivated without irrigation on the same plains where the spiny forms now occur in the wild state. It would turn deserts into fertile ranches, admitting of cattle raising, and thus restoring the lands to human industry.

The genus Opuntia is very rich in species, many of which are natives of Mexico. Here some kinds occur which have no spines at all, and others in which these organs are only partly developed. The spines of the Opuntia are of two kinds, some being broader, smooth beneath their sharp tips, and of a leafy nature; others are thin, covered all over their length by little hooks, and more of the nature of prickles. It is especially this latter kind which so often makes the Indian figs, when not carefully peeled, disagreeable for eating. Burbank transplanted into his garden as many of these deviating species as he could lay hands on, and began an extensive series of crossings. Their aim was to combine the absence of both forms of spines with the favorable qualities of the tree-like kinds of the southern deserts. Of course this could not be reached by a single cross, since numerous qualities have to be considered before a really productive thornless edible variety could be secured. Repeated crosses and selections were required, but the result has ultimately

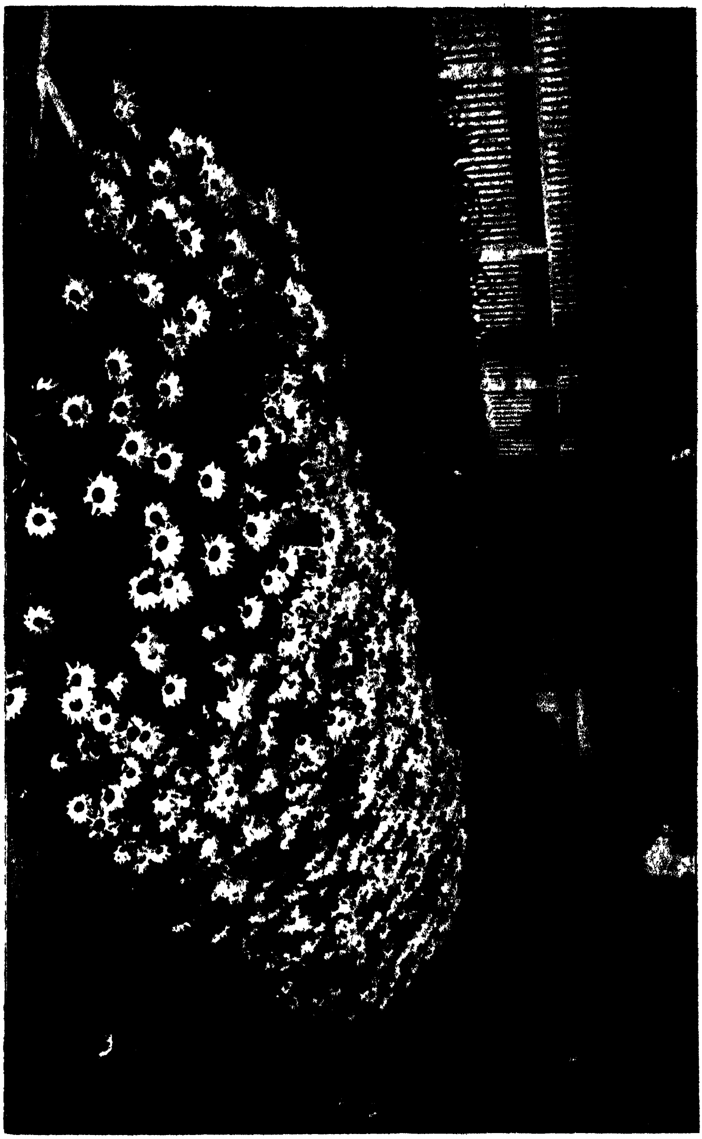


Fig. 63. A row of Burbank's Shasta Daisies.

satisfied the highest initial expectations. Some large specimens of spineless Opuntias may already be seen on his farm. They are almost absolutely smooth, and Burbank delights in softly rubbing his cheek along them, in order to give a most striking proof of their complete harmlessness. He is now propagating them, and numerous young plants may be seen on his beds, which may some day become the starting point for the desired new branch of desert agriculture.

Some of the hybrids of the stoneless prunes I have quoted as still being in the possession of small remnants of the ancestral stone. So it is also with the spineless cacti. Here and there a stray spine may be found on their stems, but being allowed to search for them, I succeeded only in securing a single one. If not absolutely absent, they are at least, so very rare as to be practically innocuous. Of course, years will be necessary to multiply the spineless cactus so as to produce the enormous numbers required to replant large parts of the present deserts. But while multiplication may be slow in the beginning, after some years it will go on so rapidly that the practical result may not be so far off as it now seems to be. Burbank gladly indulges in the prospects which may then be realized, and it seems hardly possible to overestimate the greatness of the benefit he will have conferred upon mankind.

As another instance, the Shasta daisies may be cited. On meadows, some large flowering kinds of daisies, or marguerites, are often seen, covering the green carpet like a fine white cloth. They are as bright as many good garden flowers, but on account of their commonness as wild plants, they require some improvement before being capable of attracting attention on introduction. They belong to the genus Chrysanthemum, which includes the Japanese marigold and other ornamental species. Burbank has introduced into his farm cultures a Japanese species closely related to the mar-

Fig. 65. The crisp-leaved hybrid Heuchera.

guerites of the meadows, but surpassing them by the dazzling whiteness of their flowers and some other striking qualities. These he has crossed with the English daisy, which has large flowers and stiff stems, and with the American daisy of the New England states, which is tenacious of life and hardy of constitution, but not very white. By crossing these three,

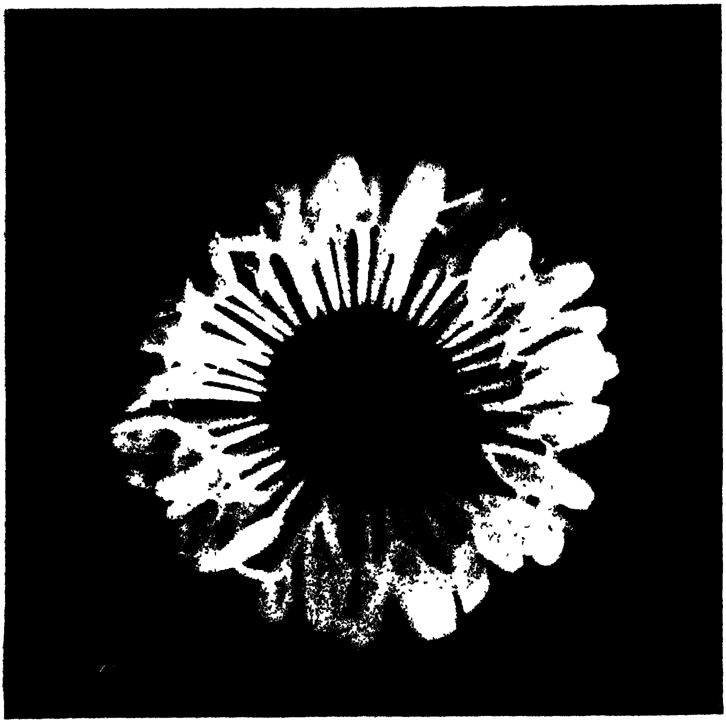


Fig. 64. A flower-head of the fluted variety of the Shasta Daisy.

he has brought about a wondrous degree of variability, ranging from small, button-like flowers to others of the size of a hat. Selection thus being made possible in different directions, Burbank chose that of increasing the size, combining with it other valuable qualities. The tall, stiff stem of the English species, the bold white flowers of the Japan-

ese form, and the abundant bloom of the American sister have given the basis of the combination. After this, selection was made for size and shape and superior whiteness, and a variety was produced in which the green tufts of foliage were covered during a large part of the spring and the summer with crowded, bright white blossoms. This new and, on account of its easy propagation, cheap garden flower received the name of Shasta daisy, after the snowy mountain of that name in northern California.

The European marguerites are well known for their high degree of variability, and they have transmitted it to their hybrid progeny. In combination with the characters derived from the other parents, this fact opens the possibility of producing a considerable number of secondary types. One of them excels by nicely cup-shaped flower heads, another by tubular ray-florets. Some show a tendency to become double, and in others, valuable, or at least curious marks, are still awaiting selection. Long rows of these bright blossoms were in full bloom at the time of my visit, and many of them were marked by little ribbons in order to save their seed separately afterwards.

The Heuchera may be cited as a parallel with the Shasta daisy, though their culture is only in its beginning. The garden species of this genus, Heuchera sanguinea, has long but slight spikes of small bright flowers of a blood red color. It is not a very striking plant, making beautiful tufts only by very successful culture. It affords a promising material for amelioration, but unfortunately, its wild congeners are very inconspicuous plants with pale greenish or small white flowers. Burbank, however, discovered, on one of his excursions through the Californian forests, a local variety of the common Heuchera micrantha. This is a nice little plant, growing abundantly along the rivulets in the woods. He found a plant with crisped leaves and decided to combine

this most beautiful form of the foliage with the red blossoms of the garden species. He transferred the plant to his garden, crossed it, and, at the time of my first visit, had thousands of young seedlings, among which he selected those which, by the curled form and brownish color of their first leaves, already indicated the success of his combination.

In the same way, Burbank has tried to improve garden plants by the introduction of some new type and by working it "into the strain" as the phrase goes. As a last instance his amelioration of the garden Canna may be quoted. Everywhere in our gardens we may now admire, besides the old species and hybrids of Canna, which are still cultivated for their large and beautiful foliage, the newer varieties of so-called flowering Cannas. Their foliage is relatively low but crowned with large clusters of red and yellow flowers. They occur in two types, the French type or that of Crozy, and the Italian type with its orchid-shaped flowers. Burbank has improved these by the combination of their qualities with those of a native American species, Canna flaccida. Thus resulted the Burbank Canna, which soon found its way into the gardens on account of its giant, orchid-like flowers. Its upper petals measure fully seven inches across and are of a rich canary yellow with carmine spots. A second hybrid of the same origin was the Tarrytown Canna, notable for the great abundance and richness in color of its flower spikes.

Many other instances could be adduced, since it is Burbank's custom to extend his experiments over as many species as he can possibly bring together in promising varieties or specimens. Unfortunately, the evidence which is necessary to insure scientific value to the practical experiments is not always easily obtained. From a practical point of view, there is no reason for publishing it, and when it is given in catalogues or references, this is often done for

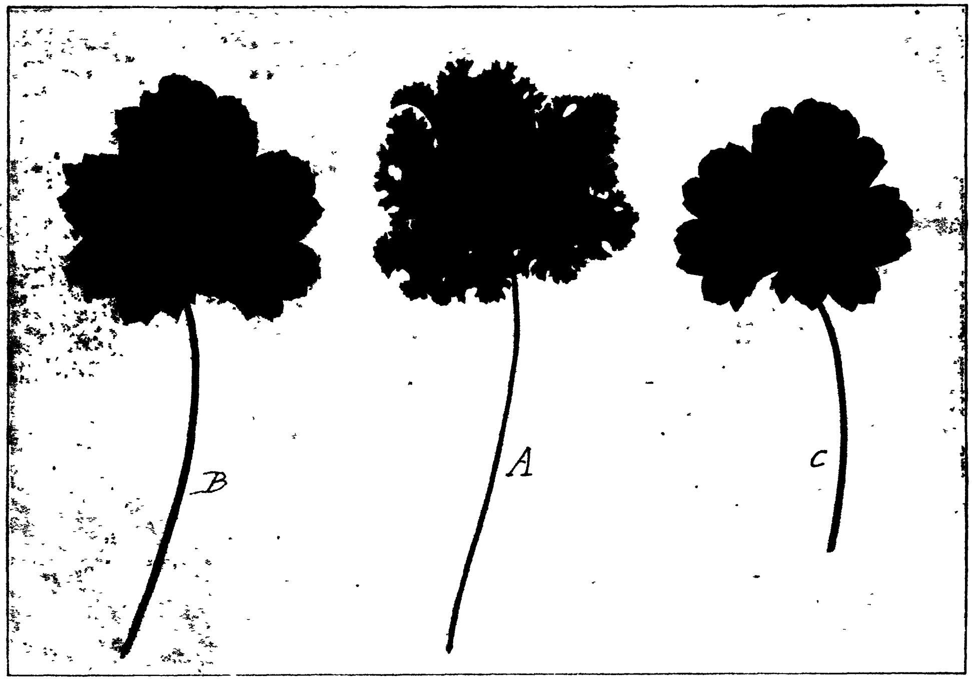


Fig. 66. A. The crisp-leaved hybrid Heuchera of Burbank. B, C. Normal type of Heuchera leaves.

the purpose of illustration only. The fruit-grower and the amateur cultivator of garden plants are quite satisfied with the visible qualities of their new varieties, and the question as to their origin has, as a rule, but small interest for them. It is to the personal kindness of Burbank that I am indebted for most of the details concerning the scientific side of his cultures, and, of course, my visits were too short to touch upon all the questions exciting a similar interest.

It seems to me a fact of high scientific significance that combinations of characters can be obtained by crosses in almost all the arbitrarily chosen directions or degrees, but that new character-units are either never produced or at least so rarely that an artificial origin is hardly beyond legitimate doubt. Concerning the combinations of characters, the investigators of the last decade have discovered distinct laws which, however, in large part, are related to varietal marks. Real specific differences must, of course, also obey distinct laws in their combinations, and the invariability of some of Burbank's hybrids, as for example the primus-berry, shows these laws to be more narrowly circumscribed than is usually assumed.

C. HYBRIDIZATION AND SELECTION

Apart from the clear and simple cases we have dealt with in our last lecture, the ordinary aim of the hybridizer is to upset the constancy of his plants, and to bring them into a state of unstable equilibrium which in the end will result in an extreme chaos of forms. From this chaos, he makes his selections, and if they do not at once comply with his wishes, he continues his crossings in order to widen still more his range of types. In doing so, he is careless about the real source of the improvements he obtains. He knows the origin of his groups and strains, but rarely that of their single constituents. Or, to put it into a simple phrase, if

his hybrid family is the result of the crosses of six or eight or perhaps more original species, he does not care whether a given individual of that family has all those parents in its ancestry or only a few of them. The visible features of the individual hybrid often point to an origin from definite parents among the group. It may have the foliage of one form, the branching of another, and these combined with the flowers or fruits or the productiveness of two or more others. Its pedigree may thus be guessed at, and for all practical purposes this is quite sufficient. But in most of these cases a scientific treatment is excluded, since exactly that which we should want to prove, is simply assumed on the ground of relatively loose probabilities.

What the breeder is very careful about is the choice of the starting points for his work. Species, elementary species, varieties, individual excellences, have to be tested with the utmost care before being allowed an introduction into the strain. For the crossing with indifferent types would increase the work without affording any real chance of progress, and species possessed of some undesirable character might, of course, transmit this to the hybrids, as well as any favorable quality. They must be excluded at the outset, and this requisite is of so essential a nature that it may be said that half of the ultimate result depends upon the initial choice and only the other half on the success of the ensuing hybridizations.

This rule is often stated by saying that half the battle is won by the first selection. From it we may deduce a confirmation of our conclusion in the last chapter, viz., that the results of hybridizations consist in the combinations of given characters, and not in the accidental production of new ones. All depends upon what is already present, since simply the new grouping is the source of the almost inexhaustible variability.

On the farm at Sebastopol I saw long rows of Calla, all richly flowering and showing an astonishing amount of variability. High and dwarf forms and all their intermediates, large and small cups, varying from white to yellow and not rarely spotted, leaves of all forms and color, some hairy and some smooth, some of a dark green and others spotted or even striped with white, more or less purple and brown, and with many other differences, too many to be here summarized. Add to this various degrees of hardiness and frost resistance, a prolonged period of blooming, rapid propagation by means of side shoots, and other qualities that may cause the varieties to become some day quite ordinary garden plants and you may have some idea of the almost inexhaustible range of variability. If we now ask whence this large group of characteristics comes, the answer is readily given by the history of the culture, but whenever we ask for the ancestry of one single striking plant, it is not historically known, but must be derived from its apparent affinity to some among the ancestors of the whole family.

Burbank began his work on the Calla with the ordinary cultivated species, which is almost everywhere known under its names of Calla æthiopica or Richardia africana. He secured the commercial varieties, including some dwarfs and some spotted forms, hybrids whose parentage seems to have been forgotten. From their crosses he secured a fragrant variety with a pleasing perfume. It is of a semi-dwarf stature and is one of the most freely-blooming kinds within the old range of forms. Under the name of "Fragrance" it has found general recognition, especially among eastern florists. The range of possibilities in this group was, however, very limited and seemed in the main to be exhausted. Therefore, Burbank decided to widen it by the introduction of new species. Here one of the most striking features of his method may be observed. If we consult the history of

Fig. 67. The tiny, perfectly formed Calla, by the side of the one of normal size, has been bred downward to show how plants may be reduced as well as enlarged in size. The small one is less than an inch and a half across.

the most famous among the older species of garden flowers and their hybridizations, as for example the Begonia, the Amaryllis, the Gladiolus, and many others, we find that progress has, in the main, been slow, advancing only by more or less accidental leaps. These advances were the result of the discovery or introduction of new promising species and of their being worked into the strain. They often mark distinct periods in the progress of these hybrid families, and not rarely they have been achieved by different breeders. In such cases, the history of the whole strain may be more or less easily traced. Opposed to these successive introductions of new species into a hybrid family, is Burbank's principle to start at the very outset with as many promising species as possible, in fact with all that may be available in any nursery or botanical garden, or may be collected in their native haunts in any part of the world. The Callas give a beautiful instance of this method, five new types having been added at once to the original stock. Of course, each of them has brought its peculiar character of flowers, foliage, and mode of growth, and an almost endless range of combinations must be the result. Calla hastata is a yellow species from the Congo; Elliottiana is of a still richer and darker yellow and has spotted leaves; Pentlandi is yellow with a dark purple spot; Rehmanni is pink on the outside and rose purple with a crimson spot within; Nelsoni is small, pale yellow and purple. All these new types have been variously crossed among themselves and with the old white kinds. Of course, the crosses were made partly with definite combinations in view, and partly as occasions were offered, and the seeds of the crosses were saved and sown in mixtures. Each single hybrid of the next generation manifestly had only two parents and thus a second and even a third season of crossing were required to obtain combinations of a higher rank. Thus the range of varia-

bility has steadily been increasing, and it may be doubted whether it had already developed all of its possibilities at the time of my visits. Some of the forms have been put upon the market, as for example the "Lemon Giant" which is said to be a cross of the albo-maculata and the hastata. Others are still awaiting selection and recrossing, but are already showing combinations and extremes of character which are new to the family. Among them bulbs of ten inches across and eight pounds in weight, with leaves of proportionate size and vigor, may be mentioned. Each year the finest flowers and the easiest-growing plants are selected for the new crosses, in order to exclude all combinations that would not contribute, in the end, to the main purpose, viz., the production of rich garden plants of easy cultivation and rapid propagation.

The same aim is pursued in the case of most of his other attempts to improve flowering plants. The size and richness of colors and designs of the European hybrids of Amaryllis can hardly be improved, but they are greenhouse plants, requiring a number of years for their development and are slow in their propagation. In the beautiful climate of California, they may, however, become changed into garden plants by first cultivating the best commercial hybrids in a greenhouse, and placing their pollen upon the ordinary, almost unimproved varieties of the garden. By sowing the crossed seed in the garden, the weakest and most unlikely specimens are soon excluded, and only those remain for repeated crossing which have inherited a sufficient degree of resistance. Then Burbank worked for more abundant bloom, more flowers to the scape, and more scapes from the bulb, an earlier and more lasting blooming period, and lastly, for a more rapid multiplication in the vegetative way. I inspected a bed of fine bulbs of Amaryllis on the farm near his house. Some of them had almost no side bulbs at all;

others had produced some ten or twelve during the summer, and in the extreme instances this number amounted to 20 to 24 young bulbs on one plant. These were marked for selection, and their seed pods gave proof that they had already been crossed with others, in order to combine their abundant and easy propagation with the finest and most showy flowers.

Similar results were arrived at with the Gladiolus, of which, however, hardy garden varieties had already been secured in Europe. But the stems were too weak, the flowers too distant, the petals too narrow, and all those deficiencies had to be eliminated by crossing with suitable parents. Some new species were introduced from South Africa, and during ten years, about a million hybrid seedlings were raised. Among these quite a number of new forms have been chosen, being hardy plants for the open air with stiff culms and densely crowded spikes of large bright flowers.

Experiments of this kind have been quite numerous. Some are of older date and had already been concluded before the time of my visits. Others were of more recent date and some only in their beginning. From the long list of species treated in this way, a few may be chosen to give a still better idea of the methods followed. One of his most notable achievements is the amelioration of the wild California tiger lily, Lilium pardalinum. This is a species which grows abundantly in many of the redwood reserves of California, bearing its large curled flowers of a fiery red on stems four or five feet high. It is remarkable for being very rich in sub-species and varieties, and almost every locality where it grows is said to have its own type. Burbank collected as many of them as he could, and crossed them with the cultivated species and hybrids of our gardens. Hundreds of thousands of crossed seeds were produced and the bulbs grown from them showed a diversity of blooms and colors greatly exceeding that of the previous stock. Repeated

crosses had to be made, and the ultimate result was the combination of the best features of the older garden lilies with the typical form of the California species. Many of the known lilies of the world have brought their peculiarities for the enrichment of the native form, and from half a million bulbs some few were in the end selected as the most promising and were given to the trade. All the remainder of the bulbs were burned, with their stems and flowers, in a great bonfire.

The clematis has produced a hybrid with bell-shaped flowers of beautiful colors. The columbines have resulted in a variety without spurs. The Californian poppies, which are highly variable as a wild species, have been asked to widen the range of their flower colors, embracing orange, white and purple, and almost all intermediate shades. Common poppies (Papaver Rhoeas and allies) have produced not only red and white, striped and spotted varieties, but also a new one of a pale purplish blue, which, in itself, was a quite insignificant flower, but full of promise of breaking up the existing range of colors and giving, by continued crosses, new combinations and new shades outside of what is already known in this group. The scented tobacco with its large white flowers, which open in the evening, has been crossed with the Mexican Nicotiana glauca, a vigorous shrub with huge clusters of flowers, which, however, are of a pale green color. The combination had in view the production of a perennial and richly blooming variety with the odor and the bright flowers of the affinis parent.

One of the most notably difficult crosses is that of the common opium poppy with other species of the same genus. Ordinarily the crosses are infertile, and success is thereby excluded. Burbank tried to cross it with the Papaver orientale, a perennial garden plant with very large and showy flowers of a fiery orange red. Like the opium poppy it is

extremely rich in garden varieties and thus affords excellent material for hybridizations. The affinity between the two species is very small and the crosses have only succeeded in one direction. The oriental species does not accept the pollen of the somniferum even if it is placed upon its stigma, but remains wholly sterile under its influence. The reciprocal cross in which the oriental is the pollen parent, produces some few seeds, but from these hybrids arise with a remarkable degree of variability in their foliage and flowers. The hybrids themselves are also almost sterile, some producing no flowers at all; others only small ovaries or miscarried ones reduced to a sharp point on the top of the flower stalk. They can, however, be fertilized with the pollen of the opium poppy, and by doing so a second generation of hybrids has been produced. This generation grew by the side of the first one on a bed of Burbank's home farm, when I visited him, and was seen to be extremely variable in its foliage and in its manner of growth, whether annual or perennial. Each individual was typical, having all of its leaves of the same shape, color, and hairiness, but among them hardly any two were alike. Selection must still be made, and the selected individuals must be crossed again in order to secure still more beautiful garden flowers.

I am now coming to the description of the most celebrated of all Burbank's crossings, those of the plums. In a large portion of the southern states, where the European varieties of plums had yielded only failures, notwithstanding long and careful attempts, the new hybrids are claimed to make plum-growing possible. In many parts of California plum culture is said to become more profitable by the introduction of some of Burbank's hybrids, and a new epoch of fruit-tree growing has thereby been opened. Hardiness and productiveness are the main features by which these results have been secured, and they themselves were obtained by the combina-

tion of the characters of Japanese and native American species, with the flavor and fleshiness of the older cultivated sorts. Some of his best hybrid and introduced varieties may be named and briefly described, according to the claims of their originator. "Abundance" and "Burbank" may thrive almost everywhere. They are capable of resisting frost during the period of blossoming. The "Burbank" is said to supplant the older varieties over large regions and may even be cultivated in districts where plum culture was formerly impossible. It has been exported to South Africa, Australia, and New Zealand, and many thousands have been planted in these distant countries. It has proved to be the most reliable plum, as well for household purposes as for canning and shipping. "Sweet Brotan" is another successful hybrid, and "Satsuma," an introduced variety miscarries in some districts, but yields a large harvest in others. About twelve years ago, the giant prune was introduced. Others are younger, and almost every year some new ones are placed on the market. Their total number now exceeds a dozen. Of the youngest varieties the fruits are not yet on the market, and only cuttings or young trees are for sale. In some cases companies have been organized with the aim of propagating and multiplying one of Burbank's hybrids, in order to distribute thousands of trees at the first moment of introduction to the public. The Maynard plum may be cited as an instance.

Ordinarily, Burbank sells the whole variety and leaves the propagation and sale to other men. The result is, that of his previous hybrids, nothing is now to be seen on his farm. The visitor sees hundreds of trees, each grafted with from twenty to forty or often more hybrids, all of which are awaiting trial and selection. Here the prunes of the future are growing, but of course they are rare instances among the thousands of good and palatable fruits that will have to

be rejected. The casual inspector cannot discern them, and moreover he is simply bewildered by the profusion of luscious fruits which are tempting his eyes and palate on all sides.

Among the American species of the large plum genus, the beach plum or Prunus maritima plays a prominent part in Burbank's crossings on account of the small demands it makes on soil and water. It is one of the most common shrubs along the eastern shores, growing everywhere on the coast or along the larger rivers, in dense bushes. It is very productive and is satisfied with almost any life conditions. It thrives as abundantly on dry and sandy plains as where the soil is covered by salt or fresh water during part of the year. It abounds in varieties having red or blue or yellow prunes, sometimes large and sometimes small, ripening early in some localities and late in others, affording thereby a rich material for selection and hybridization. The prunes are often as small as huckleberries and are gathered only for preserving purposes, but it blooms a month after most of the other species and is thereby almost free from the danger of having its blossoms destroyed by frost while it proceeds with the ripening of its fruit until late in the fall.

All these notable qualities Burbank has tried to transmit to his hybrids, combining them with the usual requirements of palatable plums. By successive crosses and corresponding selections, the bush form of the beach plum has been eliminated from the hybrid strains, upright trees having been preferred for the further crosses. Stones as small as those of the cherry, in plums of full size are another result of these combinations. The first generation of the original crosses were, of course, only of relative value, but by recrossing them with as many varieties and hybrids as were available, an extremely rich material for selection has been secured.

In some cases, the history of the succeeding crosses may still be traced, although of course the selection has steadily eliminated some characters and augmented others. But wherever the pedigree is historically known, the explanation of the different characters of a hybrid and their reduction to those of the single parental types is, of course, more reliable than in the ordinary cases. As an illustration, Burbank has described the pedigree of his Alhambra plum. It is a combination of seven distinct parents, some of which are of American, some of Japanese and others of European origin. Among the latter some are probably the offspring of old and long-forgotten crosses, thus making the pedigree still more complicated. Each generation requires about three years, the seedlings being grafted in their first summer on old trees and thereby being brought to blossom at a very early period of their life. The whole pedigree includes, by this management, only thirteen years. The initial cross was made between the Kelsey plum and Prunus Pissardi, an ornamental tree with a dark purplish foliage but without edible fruit. The offspring of this cross was fertilized with the pollen of the flowers of the French prune, and the threefold hybrid thus improved was destined for still further combinations. For these, in the meantime, hybrids had been prepared in order to bring the desirable characters of two new forms into the strain by means of a single cross. First a hybrid of Simoni and triflora was used, and the offspring obtained in this way was fertilized with the pollen of Americana x nigra, bringing up the total number of the constituents to seven. Of course, the offspring of this last cross was utterly variable and among it the Alhambra was chosen as the best.

Summing up the main lines of this historical sketch, we may put them into the following pedigree:

```
Kelsey......x...... Pissardi
            |
            a.....x French prune
                  |
Simoni x triflora......x.....b
                       |
                       c......x Americana x nigra
                              |
                           Alhambra.
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It seems hardly necessary to point out that the Alhambra has neither been the only result of this pedigree nor that the crosses in its ancestral line have been the only ones performed. Quite on the contrary, this pedigree is only to be considered as one of the hundred or perhaps thousands of diverging lines by which the main types and their numerous subordinate varieties have been combined with one another. The result has been an utter chaos of mainly excellent kinds of prunes such as it was at the time of my visits. Of some of them the pedigree could be traced, but there were many of doubtful superiority, for which it would not be worth while to keep the historical record.

The selection, of course, must be performed chiefly during the few summer weeks when the branches of the grafted trees are loaded with ripe fruits. It is a most curious sight to see on one and the same tree, branches with foliage of different colors and forms, some growing slowly and some already covered with side branches and bearing red, yellow or blue, flat and round, small and large, ripe and unripe, sometimes only half-developed fruits. The total result is strikingly bizarre. When the fruit is ripe, Burbank walks along the rows of trees, marking those which are either decidedly best or useless as far as can be judged by first examination. Then his foreman removes all those which have been marked as valueless, leaving only about half of the stock and making space for new seedlings to be grafted

Fig. 68. A. The plum. B. The brown-leaved Prunus Pissardi, two species grafted on the same tree.

on the old branches. Afterward, the remaining fruiting branches receive careful investigation. Their number reaches many hundreds each year, the total sum of all his hybrids amounting to some three hundred thousand, and having afforded the selection material for nearly twenty seasons. The comparison, of course, is based, in the first place, on the inspection of those hybrids that are ripening their fruit at the same time. But the best types of previous years must be used as standards in the work, most of them bearing fruit for a second or third time, and thus facilitating the comparison. Finally some four or five are selected as being ready for the trade, and these are then multiplied as rapidly as possible and offered for sale.

The remainder, after the extirpation of all minor forms, yields a harvest of hybrid seeds for the next sowing, and are themselves destined for renewed crosses in the following year.

In his selections, Burbank is guided by a special gift of judgment. By virtue of his long study of plums and by the comparison of so many thousands of varieties of them, he has acquired a rare and comprehensive knowledge of all their qualities, which enables him to tell on his farm, which kinds are the best for shipping, which for canning purposes, which will be household fruits, and which good for drying. He knows his trees, observes their behavior during the winter, pays attention to the vigor of their growth and the mode of their development, and from the inspection of all these qualities, can distinguish the hardy varieties from the unresistant ones, and predict for each the region and the life conditions under which it will probably thrive. To a large degree his choice is guided by such considerations, and anyone who has a lesser experience in the selection of prunes can hardly understand how it is at all possible to choose the right kinds for their distinct uses, but the success

which his creations are said to have had in the United States, and even in many countries of the old world, is the best proof of the reliability of his judgment.

This judgment is due partly to his genius and partly to his broad experience in all questions of practical plant breeding. But its application to a definite group of hybrids rests chiefly on the study of that group itself. His experience with plums will enable him to make faster progress in the study of hybrids of any other genus, but it is of no direct avail for the practical work with them. More than once in our discussions, Burbank has laid stress on this point, asserting that each new family has to be studied anew, and given the same care and devotion, in order to learn all about its qualities and possibilities. There are, of course, some general rules, but the ultimate result is mainly dependent upon a thorough knowledge of all the characters which may have or may afterward gain some influence in directing selection.

All these considerations are, however, related to the work of crossing and selecting, which, as we have seen, is only the second part of the whole study. The first part, insuring half of the result, is the primary choice of the varieties to start from. These have to include as many profitable qualities as are at the time available, but this part of the work is manifestly to be continued along with the crossing. He must be constantly on the lookout for new types, and whenever attention is directed to newly-discovered species, or when the study of the strains points to desirable qualities which may be secured by the use of older native forms which have not been tried until that time, new introductions must be made. By increasing the number of the parent species, and thereby that of the available characters, the range of variability is considerably widened, and numerous possibilities of new combinations are opened. From this point of view, I now mention the introduction of the cherries

and the apricots into the hybrid plum families. The cross between the cherry and the plum was readily made, and the hybrids were abundantly fertile. A new element was introduced by two evergreen cherries, one of the Pacific coast and one from Mexico. These were easily crossed, both with deciduous cherries and with plums, but the results are still awaiting selection and improvement.

The hybrids of the plums and apricots are called by Burbank plumcots, and a certain number of these most delicious and beautiful fruits I have seen on his farm at Sebastopol. They have the outer appearance of apricots but combine the rich and varied colors of the prunes with the soft indument of the former. Dark blue and downy apricots are as striking a novelty to the eye as the combination of the flavor of prunes and apricots in one fruit is flattering to the taste. Some had a yellow fruit flesh, in others it was red or pink or nearly white. The dark red varieties seemed to me the most juicy, and were, perhaps, to be the next to be definitely selected. Some plumcots have free stones, but others were cling stones. In many other respects, striking differences were observed, giving an almost complete material for his selections.

It is difficult to tell whether the range of possibilities of the crossings of plums has reached its ultimate limits or whether it will afterward assume still more astonishing aspects. The cross between apricots and the Japanese plum has been attended with difficulty, and has succeeded only by the use of distinct varieties. Peaches should next come up for trial, but their crosses with plums have been devoid of success until now. But perhaps some of the hybrid strains may be more suitable than others, and new attempts may succeed where older ones have miscarried. In case of success in this new line, the range of possibilities will become almost inexhaustible.

Leaving our sketch of the historical evidence given by Burbank concerning his hybrids, some points of biological interest remain to be mentioned. In the first place, crosses are by no means always successful. The result depends mainly upon the affinity of the chosen parents. Whenever their systematic differences are too great, the cross will be infertile, or at least the produced hybrids will refuse fertilization, even with the pollen of their parents. Repeated crosses are impossible and no practical results can be obtained. Or all the hybrids may be of inferior quality, not promising any improvement and thus are not worthy of further culture. Of this, Burbank gives an instance in an experiment with a Californian dewberry. He transplanted a specimen of this indigenous species into his garden, isolated it, and brought to its blossoms the pollen of almost all its allies he had at that time under cultivation. He gave it the pollen of brambles and raspberries, of strawberries and roses and even of cherries, apples, and pears. All the seed was saved in a mixture and a strange lot of hybrids arose from them the next spring. Some repeated well known types, but many seemed full of promise of new forms. At the blooming period, many defaulted, making no flowers at all, and the remainder proved to be utterly sterile; no single hybrid could be chosen by which a new strain could be obtained.

A parallel instance is that of the Nicotunia. This is Burbank's name for a hybrid he once won between a tobacco plant and a Petunia. The parents are so distant that, as a rule, the cross never results in good seeds. Among hundreds of seedless capsules, he found one in a better condition, and from its contents raised one single plant. This, however, was an annual and absolutely sterile and so the experiment ended with its death.

A last point which we have to discuss is the interest

attached by the practical breeder to the purity of his fertilizations. Of course, in scientific investigations, the father is of equal importance with the mother, and the utmost care has to be taken that the stigma is covered with pure pollen. Moreover, in the pedigree, the lines of the male ancestors require the same care as the female line. Exact and elaborate book-keeping is the rule, and no single pollination should be made that is not thoroughly controlled and registered.

In practice, however, such a susceptibility would be as impossible as useless. The proof of the pedigree is not the aim of the experimenter. He only looks for the result. In crossing six or seven species and hundreds of their hybrids, the pollen is brought from one flower to the other, as opportunity is offered. Hundreds of crossings may be made in a few hours, and their seed may be saved in mixture without special care, or too much loss of time. If, however, each of these crosses has to be kept separate, to be labeled and registered, and its seed sown apart from the others, the amount of work will increase a hundred-fold without any chance of giving more or more profitable hybrids.

Separate pedigree book-keeping being thus impossible, small impurities of the pollen cannot be avoided and are not to be noticed. Pollen is brought by the finger to the stigma, but a breeder would simply laugh at the idea of a scientific investigator washing his hands between successive pollinations, or inspecting his fingers with a lens in order to remove some stray remaining pollen grains Quite on the contrary, such unintentional crosses often bring greater chances of unexpected success than the regular and contemplated pollinations, and if, perchance, they give hybrids of inferior quality, the damage is only small, since the offspring is sure to be eliminated by the next selection. Thus we see that some freedom must be allowed in the choice and in the purity of the pollen. But, on the other hand, it is easily seen that much

caution is to be observed in the scientific interpretation of the breeder's results.

As a general rule, we may state that the broad lines of practical hybridizing and selection afford highly valuable resources for theoretical discussions, but that on single points they should not be accepted as definite proofs, but only as indications for more sharply circumscribed experiments. Even with this restriction, however, the value of Burbank's work for the doctrine of evolution, compels our highest admiration.

D. MUTATIONS IN HORTICULTURE

For the larger number of horticultural varieties we do not know the origin. Many of them are older than the historical records, others have been found in the wild state or in foreign countries or in old-fashioned gardens. A certain number appeared in nurseries and cultures, but their first generations were overlooked and they were appreciated only when it was already too late to study their first appearance.

Whenever this first appearance has been noted and recorded the development of the variety took one or two or a small number of years. Sometimes it appeared with the full display of its qualities and proved constant from seed from the very beginning. But such cases are rare. Ordinarily it was discovered, at first, in a very imperfect and often scarcely perceptible degree of development, or it was not constant from seed. In both cases it had to be developed by selection in order to insure a normal degree of purity and constancy. This process requires some years, and their number is different for different species, according to their capacity for self-fertilization, their fertility, and other factors.

Whenever the varietal mark is plain in the first year, selection has only to produce constancy. This might be attained at once, if the visits of insects could be excluded,

either by isolation or by covering the flowers and fertilizing them artificially. If this is done, the varieties prove constant, with few exceptions. In practice, however, isolation and artificial fecundation are often too cumbersome, and the easier way by repeated selection is preferred. Gradually it eliminates the effects of the natural crosses with the neighboring varieties and in three to five years it ordinarily brings the purity up to the degree required for commercial purposes.

If, however, the varietal mark should show itself only imperfectly in the beginning, being limited to a supernumerary petal, to a slight indication of a new color, to a fine line of a different hue, or to a hardly perceptible fragrance, selection has to improve it. In the case of pure and artificial pollination the ordinary variability of the new mark would bring it to its main condition as soon as the sowings reach the required extent, but in practice the process must be combined with the described gradual elimination of the effects of crosses, by which it is, of course, made much slower. Four to five years, however, are, as a rule, sufficient to reach the aim.

The way in which all these varieties originate is best expressed by the technical term of *chance seedlings*. Fruit-growers, nurserymen, and amateurs are always on the lookout for such. Even among the commercial growers there is a regular search for deviations in the direction of improvement. Any seedling that chances to show more desirable characters than the average will be noted and cared for. To this discriminating search is due the superiority of some of the leading varieties of fruit-trees, which have been recognized as meeting special requirements and have been multiplied accordingly. Such chance seedlings occur everywhere, from time to time, but the cause of their appearance is, as yet, wholly unknown. The only thing we know about them is that among large numbers the chance of finding

them is greater than in small cultures. In small private gardens they are very rare, but in large nurseries they will hardly ever fail, although they may often be much rarer than, for example, one in a year.

Hybridizing being one of the most important procedures in many of the larger nurseries, the question has often been raised whether such chance seedlings should be more frequent, or rarer, after crossing than in pure strains. Of course, this question is of the highest practical as well as scientific interest, because if it had to be answered in the affirmative, at least one possible cause would be indicated. It seems quite possible that such should be the case, and even our knowledge concerning the numerical laws of the splitting of a hybrid progeny does not exclude the possibility that among a thousand and more offspring some chance deviation may occur. As yet, however, the evidence at hand is too rare to justify a definite conclusion.

In this respect the same conditions prevail on Burbank's farms as everywhere else. Of course, sports occur quite often and, in many cases, may even be produced at will. But sports include a wider range of variability than the chance seedlings. The latter can always be considered as sports, but not all sports belong to this same group. A critical review of some of the most interesting sports among the cultures of Santa Rosa and Sebastopol will best prove this, and at the same time it will give an opportunity to convey a still clearer idea of the bearing of Burbank's methods and results on the science of evolution.

In the first place, the occurrence of elementary species in nature often opens definite possibilities for culture and selection. Burbank showed me a highly interesting sport of a Mahaleb cherry or Prunus Mahaleb. It grew in a little grove of shrubs of the same species, on his Sebastopol farm. It had yellow berries instead of black ones and showed some

corresponding smaller deviations from the average type. He uses the species for stocks for grafting and had sown them from seed which he had received from the southern states. From one of these introduced seeds the sport had arisen. There could be no doubt that it was due to a real mutation, and it was manifest, also, that this had been produced before the introduction. But whether the deviating specimen itself was to be considered as a mutant, or whether, perhaps, in the original locality an old yellow variety of Mahaleb cherry existed, he could not tell. It was noticed here for the first time, but whether it was old or new, nobody knew. It was, however, a most typical sport. Elementary species among trees have not yet been given the interest which they deserve. The apples, pears, hawthorns, and some others have yielded numerous types, either for industrial culture or for scientific description. Oaks and walnuts differ in the same way, and there can hardly be any doubt that this is true for a large number of deciduous and even of coniferous trees, also. A scientific distinction and industrial test of these elementary species might probably lead to a distinct improvement of many of our forests and groves, giving more uniform crops of nuts, or harder and better lumber, or a more rapid growth, or more straight and less branched stems, etc. A combination of the results which Nilsson obtained by his sharp distinction of the elementary species of cereals, with the possibilities indicated by the hybrid walnuts and other trees of Burbank, might open large prospects of improvement in forestry.

In many cases it is doubtful whether a sport is due to a mutation or to extreme fluctuating variability. The fragrant varieties of Calla, Dahlia, and Verbena may be cited as instances. The first of them has already been alluded to, but the production of the two others deserves a more detailed description. Along the fence of his garden, in front of his

house, a large row of fragrant Verbenas was in full bloom, at the time of my last visit. It was the ordinary European garden-type, but of a uniform pale pink color. All of them were manifestly derived from cuttings from one individual. They had the most delicious flavor of the trailing Arbutus, Epigaea repens, a much-beloved creeping herb of the eastern woods. Burbank told me that, years ago, when busy in the selection of his Verbenas, he was struck by a faint odor from some of the flowers. He did not, however, succeed in singling out the fragrant individual. Next year, he noticed the same odor and was able to isolate the sporting plants. He saved and sowed their seeds, got better scented specimens among the offspring and selected and isolated these. After some years of selection the fragrance was noticeably increased and the variety received the name of "Mayflower." It is not constant from seed and it is not known whether it can be made so or not. Ordinary Dahlias have a somewhat disagreeable odor. This has been driven out and replaced by the sweet fragrance of a magnolia blossom of the glauca species. The origin of this race was a single plant with a faint fragrance, which Burbank noticed, several years ago, on one of his beds. Through isolation and repeated selection the fragrance has been increased and fixed, and the variety purified from its hybrid admixtures, but, as yet, it is not sufficiently fixed to reproduce itself purely from seed. Whether the original variant was itself a hybrid between an unnoticed fragrant parent and the ordinary form, or only a minus-variant of the new fragrant variety, it is now, of course, impossible to decide.

Fragrance in fruits is often discovered and improved, in the same way, by Burbank. Even among walnuts he has produced a fragrant variety. More interesting, from a practical as well as from a scientific point of view, is the sweet walnut which lacks the bitter tannin in the coat of its nuts

and in the thin shell of its seed. As a variety it has been given the name of white walnut. Its nuts are white and do not need the artificial bleaching of the other sorts to which the tannin of the coats gives their dark appearance. The pit on the inside of the nut is of a pure white and sweet, because the astringent taste of the shell and the meat has been taken away from it. This variety was started from some of his hybrid nuts which, at first, gave some indication and promise of success in this line of improvement.

In contrast to these pure sports I now mention the cases in which a combination, obtained by means of a cross, is so strikingly different from what could be expected that it is instantly designated a "sport." The Bartlett plum is such a chance seedling among the plum hybrids of the Sebastopol farm. We inspected the tree, but the fruit was not yet ripe. It is quite different from other plums. It branched from its very base and had erect shoots with a fine peculiar foliage. Its plums have the taste and fragrance of a Bartlett pear, and even the meat resembles that of this well-known fruit. Visitors whom Burbank requested to eat it with their eyes shut, have taken it for a pear. It sprang up in a lot of hybrid seedlings, most of which had been produced by crossing the Kelsey and the Simoni, but for this individual seedling the ancestry could not be traced. It is, however, an evident combination, and all of its qualities can be traced to its probable parents, the flavor being mainly due to the Prunus Simoni.

The stoneless prunes and the spineless edible cacti are such evident hybrids that it is doubtful whether anybody would designate them as sports. I have already given a general description of them, but shall now add some details. About the year 1887, Burbank received his first "prune sans noyau" from a French nurseryman. It soon fruited and produced a fruit about the size of a small cherry. It was

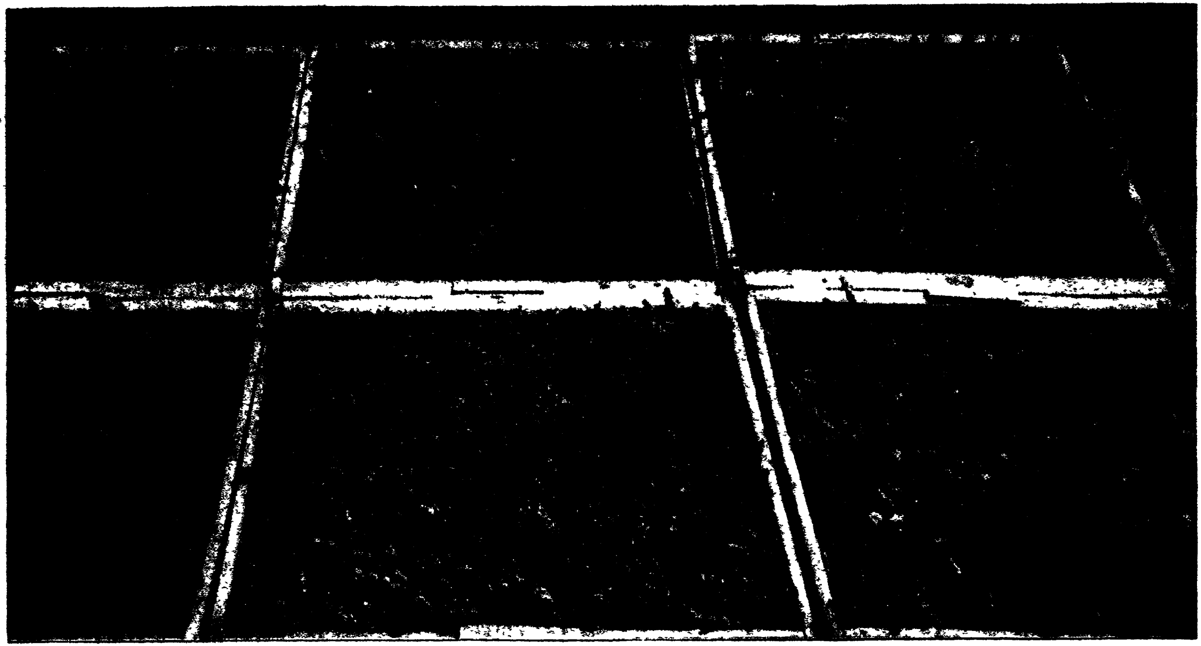

Fig. 69. Seedlings of the Spineless Cactus in their first year. Most of them are spiny, but the rare spineless ones will be selected for propagation.

crossed with the French prune, Petite d'Agen, which is widely spread in California culture, and with other prunes. About 1893, the first hybrid fruits ripened. Numerous crosses had been made, numerous hybrids had to be tested. Only a small proportion of the seedlings were stoneless, and most of these showed the undesirable qualities usually found in seedlings. It was only in 1899 that a good palatable stoneless prune of sufficient size appeared. This has been given the name of Miracle, and is now being brought into the trade by the Oregon Nursery Company, at Salem, Oregon. It combines the main character of the "prune sans noyau" with the good qualities of the Petite d'Agen, while hardiness and bearing qualities are characteristics of both parents. It does not contain sugar enough to be classed among the drying prunes, but for cooking it must supplant the well-known Damsons, being larger and more productive than any of them.

The spineless edible cactus combines, in the same way, the main character of its spineless parent with the excellent qualities of the ordinary cultivated varieties. It has excellent fruit of a new flavor which may be eaten fresh or cooked. As food for cattle the stems are very rich; they are estimated to be at least one half as nutritious as alfalfa (Lucerne clover). The production of this variety started from five species of Opuntia imported from different countries, the names of some of them being unknown at the time. Among them was a spineless, but small and insignificant, species from Central America. These he has crossed and re-crossed with the cultivated varieties, selecting for vigorous growth and superior food-bearing qualities. A number of European and African varieties of Indian Figs were sent to him and the Opuntia vulgaris, O. Engelmanni, and other hardy types were mixed with them. The beds, which I saw in 1906, showed hundreds of specimens which had been

Fig. 70. Seedlings of the Spineless Edible Cactus in their second year.

planted in the spring and had already produced a first set of numerous disc-like branches. They were expected to make two or three more sets in the same year and to fill in the large spaces which were left between them at the time of their planting. They varied in the size, form, and color of the pods, and probably, also, in their nutritious qualities, and were grown as a direct test of these points. The value of these hundreds of plants which will, on the average, produce fifty pods each in a year, may be deduced from the fact that he had sold five of the pods to an Australian firm and was building a new and larger residence from the sum they had brought him.

It would, of course, add highly to the value of this race if it could be made constant from seed. It is evident that a rapid spreading, as well as the treatment on the farms, would be made more easy by such a change. I saw numerous wooden seed boxes with small seedlings, but almost all of them were spiny. Thousands were rejected, and only those which showed a distinct diminution of their spines were selected and planted out. Large beds with young spineless plants were seen in his garden. Burbank estimates, from the present extension of uncultivated lands fit for the production of cacti, that his spineless and edible varieties may, in time, double the population of the earth. At least they promise to do more for the world, in a material way, than any other of his productions, but much work will still be required before even an essential part of his hopes can be brought into execution.

Beautiful and striking sports are sometimes offered by hybrids which revert to a quality of one or more of their pure ancestors, this mark not yet being displayed in the previous hybrid generations. An instance of this we admired among his Callas. Hitherto his hybrids had varied in the color of their spathes from white to a more or less intense

Fig. 71. Extreme variability in the shape of the leaves of hybrid poppies. Second generation from a cross between the Bride variety of the Opium poppy and the Oriental poppy.

yellow. During my last visit one of the seedlings, however, opened its sheath with a purple color, reminding us of its forefathers, Rehmannii and Nelsonii, with their pink, rose, and purplish hues. But in this hybrid the color was deepened, covering almost the whole of the flower, and was thus evidently improved.

Hybrid poppies are liable to reversions, also. Burbank crossed the oriental poppy, which is a perennial herb, with the snow-white, double and fringed flowers of "the Bride" and some other varieties of the common opium poppy. I have already referred to these crosses and their high degree of variability. On my last visit, I saw a large bed in full bloom repeating almost all the known color varieties of double poppies, and varying in many other directions. He also crossed this Bride variety and some others with a wild and scarcely cultivated smaller species, the Papaver pilosum, which has pale orange flowers. Among the offspring some were fringed and some double, but the most curious fact was that some produced colors not intermediate between, or like, those of the varieties named, but returning to the original type of the whole somniferum species. The special causes of these atavistic reversions, however, remained obscure.

Bud sports are one of the most typical kinds of sports. Burbank cultivated one of them. It was the Pierce's grape, which originated, some time ago, as a branch on an Isabella grape on Mr. Pierce's farm at Santa Clara, Cal. It is well known for its large and superior fruit. It comes true from seed but is liable to sport in this way from time to time. The sporting seedlings differed from the average in the shape, color, and hairiness of their foliage and in their mode of growth; but, at the time when I inspected them, they were still too young to produce fruit.

Other bud sports Burbank has not observed, so he told me. Of course, the sports with variegated leaves are to be

excluded. Such are common in almost all the larger nurseries. Sometimes they come from buds, sometimes from seeds. A case of the latter belonged to a hybrid between the oriental and the opium-poppy, of which he showed us three large specimens with the foliage of the oriental parent, but with beautiful pale yellow borders and streaks on the

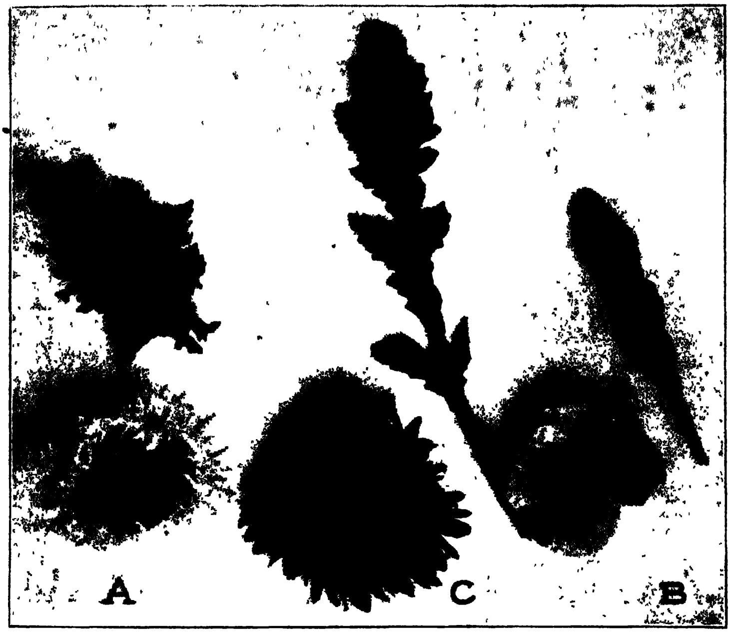

Fig. 72. A. The variety of the Bride of the Opium Poppy. B. The wild species Papaver pilosum. C. The hybrid of these two poppies.

leaves. It scarcely flowers and is wholly sterile, but may easily be multiplied by division.

Whether the thornless brambles, previously alluded to, constitute a mutation remains to be investigated. During the days of my last visit, they flowered for the first time; their long stems and numerous leaves being as smooth as when the plants were selected from the seed boxes.

A chestnut without spines on its burs was growing on the Sebastopol farm. It was a single young tree, found among the numerous offspring of a cross between the Japanese and the American species, both of which have spiny burs. It was, probably, a pure mutant.

A blue poppy which appeared in his crosses of Papaver Rhœas and allied species has already been referred to. It was, also, probably, a pure mutation, which, however, showed itself, in the beginning, only in an imperfect degree of development.

The same holds good for his scarlet California poppy (Eschscholtzia californica). He discovered the first indication of this mutation, some years ago, when inspecting large beds of ordinary yellow California poppies. One flower caught his eye; it had on one of its petals a fine longitudinal line of scarlet color. It would, surely, have escaped the eye of most other men, but to Burbank it betrayed the capacity of this one plant to produce a variety of a new and unsuspected color. He isolated the plant and saved the seed. Among the offspring the scarlet color was repeated, but still to an insignificant extent. He repeated the selection during some years until he got a race of a pure and uniform scarlet color in all the flowers and on all the plants. We saw large beds in full bloom but without atavistic reminders of the yellow prototype.

It would be a most interesting task, full of promise, to try to repeat the observation of the appearance of all these mutants and to follow their origination and their development under the rigid conditions of scientific research. It might be expected that the material from which Burbank started would, probably, repeat the mutation, even as other horticultural and experimental mutations are known to have been produced repeatedly. In doing so an exact history might be given instead of the more or less vague and incom-

-plete reminiscences of the breeder, and a basis might be worked out, from which scientific conclusions of the highest importance could be drawn. Burbank often claims that the production of a single novelty requires much time and much labor and a considerable amount of space in his garden during a series of years. The scientific repetition and description of such a mutation experiment would, however, require perhaps ten times as much time and labor as the practical production of the same variety.

In one instance I have had the good fortune of producing experimentally a variety, the exact counterpart of which has been produced industrially by Burbank. I refer to the origin of a double marigold. Burbank is doubling his Shasta daisy, and in my garden I observed and guided the springing up of a double form of the yellow corn-marigold (*Chrysanthemum segetum*). Although Burbank's description of this selection is only very short and succinct, there cannot be the least doubt concerning the parallelism of the two cases. The Shasta daisy is, as I have already pointed out, a hybrid between a Japanese, an American, and an English species of the genus Chrysanthemum. Among them, at least the English ancestor is highly variable, and it is evident that the fluted rays, and some other remarkable deviations which occurred in the hybrids, may be due to this source. The same holds good for the doubling. Ten or fifteen years ago Burbank discovered a slight degree of augmentation in the number of the ray-florets of some of his hybrids. He carefully isolated them, observed an increase in the deviation and repeated the selection until the flower heads became as double as those of any other double variety among the Composites.

In the case of my yellow corn-marigold the selection has been accompanied by the counting of the ray-florets for all the plants of the succeeding generations. The first indica-

tion was one supernumerary ray on each of two flower heads of a single plant. Sowing the seeds of this individual, the numbers were seen to increase rapidly but all the ray-florets always belonged to the outer rows of the heads. After a selection of three years, suddenly an individual appeared which had some stray ray florets scattered among the tubular florets of the center of some of its latest flowers. The seeds of this plant at once gave the desired double variety. All the progeny produced more or less double flower heads, the number of the rays ranging, in the best instances, from 100 to 200. In the following year, the race could be somewhat purified and thereby improved, but the type was not essentially changed and has since remained constant. The appearance of the first ray-florets among the little central tubes would, of course, easily have been overlooked and the increase of the number of the rays would have seemed gradual throughout. The selection would have obscured the mutation, as has, probably, been the case in the production of many other horticultural varieties.

V

THE ASSOCIATION OF CHARACTERS IN PLANT-BREEDING

A. ASSOCIATION OF CHARACTERS IN NATURE

The doctrine of evolution is so closely associated with the interests of man that each phase of its broad lines of teaching commands our special attention. Amelioration of domestic animals and plants is one of the prevailing features in agriculture and horticulture. The laws which govern these practical endeavors as well as the scientific investigations are now being slowly disclosed. Many of the common questions which puzzle the horticulturists can be answered only by appealing to these laws. The problems involved are, however, many-sided and in order to gain a distinct knowledge and a clear insight into their different methods of research it is nowadays unavoidable to divide the subject into its separate parts.

Some lines of research may guide us along the paths of anatomical and histological development; others are related to the more common but equally significant facts, which may be gathered by observations in the field. These latter are vitally related to the study of organic evolution, and often have a direct bearing on the practical processes of breeding. Agricultural plant-breeding is the evolving of useful qualities. But what are qualities and how may they be discerned and studied?

For many years this question has been considered as a very simple one, easily to be answered on the basis of our common knowledge. Of late, however, this attitude has completely changed, and the intimate nature of qualities and characters has become an object of most intense interest for the practical breeder as well as for the student of

evolution. Experience has taught that qualities are often associated with one another by distinct laws, and that a knowledge of these laws may give us a power over them, greater than any man has heretofore aspired to. Even a suspicion of the meaning of these laws, or an intuitive appreciation of their work, may lead to valuable results, if it is only combined with a thorough knowledge of the species in question.

Before going into the details of my subject I wish to convince my readers of the truth of these assertions by giving some noticeable illustrations. The first is an old one, the second is afforded by Burbank's work, and the third is taken from Nilsson's experiments in agricultural breeding. It will not be necessary to go into many details, since even without them their bearing will be clear enough.

The common stock (Matthiola incana) is cultivated in double-flowered and in single varieties. The singles are pure, but the seed for the doubles is saved on single-flowered specimens belonging to the same variety. From these seeds about one half give double and the other half single flowering plants. The doubles, however, obtain a higher price on the market, and it is therefore of some interest to separate and isolate them as early as possible. In France this is done by children, who pick out the singles and spare the doubles. This is done while the plants are very young, having produced a little stem with some small leaves, but still without branches and without flower buds. It is impossible, therefore, to distinguish them by these buds, but there are slight differences in the color and the hairs of the leaves, which separate the doubles from the singles for the experienced eye. These differences, however, are so very slight that it is impossible to put them into words or even to explain them to the layman. No botanist, as far as I know, has as yet succeeded in recognizing them, and nevertheless the

children of the nurseries are seldom mistaken in their choice. Hence, we may conclude that the character of the doubles penetrates the whole plant and produces small changes in all the organs, even at the very earliest periods of their development.

For my second illustration I choose Burbank's selection of quinces. A thorough study of this genus has enabled him to see relations between the qualities of the fruits and the characters of the foliage. Thereby it has been possible for him to judge of the value of new acquisitions or to compare the different specimens of a hybrid culture, long before the time of blooming. Thousands of young seedlings may be estimated in this way, the unpromising ones being thrown away before they have to be planted out, and by this means, of course, much space and labor is saved. The differences between the seedlings are, some of them, so great that they may be appreciated by other people too, but others are so slight that they escape general observation. But in the first case their relation to the qualities of the fruit is hidden from the eye of the ordinary horticulturist, and it is only by means of a special knowledge of the plant, and an intuitive appreciation of its virtues that Burbank could make these remarkable selections.

My third example is taken from the selection of cereals on which Nilsson, the director of the experiment station of Svalöf in Sweden, is working. The barley, as cultivated in the central parts of Sweden for the purposes of the brewers, was generally suffering from the weakness of the straw, which caused it to lie down in unfavorable summers, thereby often involving the loss of large parts of the harvest. After many years of unsuccessful efforts to improve this barley in order to give it stronger halms, Nilsson decided to solve the question in quite another way. He gave up the selection of the ordinary sort, the so-called Chevalier barley, and

proposed to look for the same qualities among other sorts with resistant halms. A minute study of the botanical characters of the ears, of their spikelets and scales led him to the discovery of a relation between the form and the hairiness of the latter and the practical qualities of the grains. On the ground of this relation tens of thousands of individual barley plants were scrupulously investigated, and some sixty were chosen out of this number for a comparative trial of their progeny. Among these the continued study during subsequent years led to the selection of the one which best answered the proposed question, inasmuch as it combined the qualities of a fine brewers' barley with strong and resistant halms. From this one plant a race has been derived, which received the name of Primus-barley and has already supplanted large parts of the cultures of the original Chevalier kinds all through the middle parts of Sweden.

These examples may suffice to convince us of the usefulness of a thorough study of the association of qualities and characters of cultivated plants. Evidently such a study is a very difficult one, but it opens new and broad lines of research. In order to build upon a scientific basis, it is necessary not to confine ourselves to cultivated plants, but to take as large a view of the whole vegetable kingdom as possible. Only in this way is there a chance of discovering the great laws of nature which govern this most intricate group of phenomena.

Broadly speaking, the characters of plants may be considered from a systematic or from a physiological point of view. The systematist explains the affinity by means of the laws of inheritance, assuming thereby a common cause for every character which remains unchanged throughout a large group of closely related species. The flower heads of all the composites must have one and the same cause, and so it is with their inferior ovary, their connate stamens, and

many other characters. This cause, though hidden from our eye, and showing itself only in its effects, must be the real character, which by means of heredity has come to be present in all members of this large family. We may assume it to be pure and simple, even if it is never allowed to show itself as such, but must always become visible in combination with the other characters of the same species, and may be changed by them to a greater or lesser degree.

Fig. 73. Flowers of columbine, showing the spurs.

The physiologist has remarked, however, that the laws of heredity cannot be the only cause of the similarity among plants. In innumerable cases there is a likeness which cannot be explained by a common origin. The spurs of the orchids and of the violets, of the toadflax and of the columbine are evidently the same organs, playing everywhere the same part of producing honey for the visiting insects. Notwithstanding their differences in size and color, and even in the manner of secreting their product, there can be no doubt as to the identity of the primary cause which has produced them. On the other hand the plants which bear them belong to such widely divergent families, that it is simply impossible to look for a common origin in order to explain this repeated occurrence of spurs.

So it is in almost every case, for characters of the highest systematic value as well as for minor marks. Inferior ovaries are found among dicotyls and among monocotyls,

gamopetalous flowers occur in the mallows and in the hyacinths, symmetrical corollas and decussate leaves are spread over the families of the natural system in the most capricious manner, and even the forms and structures of the leaves do not show any relation to systematic affinity. Assuming the same causes for the same phenomena, the physiologist is led to the conclusion, that the visible characters must be the result of internal properties which may be the same in widely different groups of plants. These internal qualities may pass from species to species by the laws of inheritance or be produced anew in distant families and genera.

The chemist tries to connect the visible properties of his substances with the assumed qualities of molecules and atoms, and to explain, by this theory, their conformities and their divergencies. In the same way, the physiologist explains the likenesses and the differences of his plants, by the assumption of equally invisible units, which are supposed to underlie the visible phenomena. These units he calls unit-characters. For him they are the resting pole in the ever-moving tide of the outward forms. On this principle he tries to explain the common features of plants, independently of the question whether they are closely related or belong to distant groups. It is a wide field for observations and inductions, but the study heightens our appreciation of the real nature of all living beings. It is a kind of biological analysis, leading to a knowledge of the intimate elements of which the plants are built up.

The study of these elements or unit-characters has led to the discovery of a most significant phenomenon. It is the regular coincidence of marks, which hitherto had been regarded as quite independent from one another. This association has been shown to obey natural laws, and the study of these laws enables us to predict one mark from the observation of the other. The relation of the color and form of

Fig. 74. The deadly nightshade, or Atropa Belladonna. A. Brown flower, and B. Black fruit of the species. C. A twig of the yellow variety with pale flowers and yellow fruits.

the young seedlings of the stocks to the shape of the flowers is only an instance of the general phenomenon of association and so it is with the marks which enable Burbank and Nilsson to make their selections.

These coincidences are called technically, *correlations*, and it is these which I have chosen for the subject of this chapter.

Some of them are of a simple and obvious nature, and their internal cause may easily be understood as soon as the association has been pointed out. Such instances may serve as a basis for further discussions, and become a guide into the more intricate cases.

It is a common experience that many color-varieties of plants may be distinguished by their seeds. This rule holds good for garden plants as well as for large crops. A dark color of the seed indicates a bright flower, a pale seed is usually associated with white or pale corollas. Stocks have grayish, brown, or bluish seeds according to the color of their petals. Among the lupins the red and blue forms may often be distinguished by their dark seeds, but the white variety has white seeds (Lupinus angustifolius). White vetches have, as a rule, yellow or greenish seeds, in contrast to the dark seeds of the common species. The true opium poppy has white flowers and pale seeds, and many other garden varieties of this plant differ in their flowers and seeds in a more or less corresponding degree.

In all such cases there can be no doubt, that the coincidence is a real correlation, and that the cause, which darkens the flowers is the same as that which is active in the seeds.

Berries often show the same correlation to the flowers. If a species has red or blue corollas combined with dark berries, its white variety will often show pale or even white fruits. One of the most interesting instances of this rule is the pale variety of the belladonna, a very poisonous plant,

Fig. 75. The long-leaved Veronica (*Veronica longifolia*).

which grows in many forests of Germany. It has brownish flowers and large and shiny black fruit, the color consisting of two factors, a yellow and a red one. A variety of this species was discovered by Schütz in a wood in the neighborhood of Calw in Würtemberg about the middle of the last century (1851; cf. Hoffman, Sp. et Var., p. 87). It has pale greenish flowers and bright yellow berries. It comes true to its character from seed, and is often cultivated in botanical gardens. The red dye or anthocyanin, which darkens the corollas of the species and is concentrated in the fruit to a degree that makes it black, is absent in both organs in the variety, the yellow not being affected by the change. Evidently the red dye is the same color in both organs, and as soon as it became latent by the production of the new form, it disappeared simultaneously from the flowers and from the fruits.

In many species this anthocyanin is not limited to the flowers and the fruits, but may be displayed in the foliage also. The stem and the branches, the leaves and their stalks, and even the bracts of buds and the coats of a bulb may be imbued with the color. It very often happens in such cases that the white or pale varieties show their marks in the correlated organs. As the first example, I choose the thorn-apples. They are known in a white and in a blue variety, the flowers of the latter being of a pale blue. The colored form (Datura Tatula) has stems and leaves of a brownish color, but the same organs are of a pure green in the white-flowering plants (D. Stramonium). Even the young seedlings may be distinguished by the tinge of color on their stem, and whenever the dark ones are separated from the pale, all of the first will bear blue flowers and all of the latter white.

It would be easy to give a list of such examples, especially of garden plants, since horticulturists often select their seed-

lings by this mark, thereby being enabled to throw out the "rogues" long before the time of blooming.

Perennial herbs may show the same correlation. In the colored forms the young shoots which arise from the rootstocks have a dark tinge, but in the white varieties they are pale or colorless. The willow-leaved Veronica (V. longifolia) affords an instance, which has proven useful in the study of the bud-variations of its hybrids. The hybrids of this plant have the same blue flowers as the parent species, but if one of the parents used for the cross was the white variety, these blue hybrids are apt to produce groups of white flowers. Such groups may consist of a few corollas upon a blue spike, or may form a longitudinal line, leaving the flowers on one side uncolored, while those on the other are blue. Or a whole raceme may be white on a plant, whose remaining spikes are of the ordinary color. Lastly, a stem arising from the root may have returned to the type of the white parent. In these latter cases the color can be predicted from the very first beginning in the growing buds, and the whole stem, with all its branches and leaves will be of a pure green instead of showing the brownish tinge of the species.

Bulbs of hyacinths may seem to the layman to be all alike, but the breeder is often able to distinguish their varieties by their size, the number of their little side bulbs, the form of their top, and especially the color of their outer coats. The correlation between the marks of the dry and marketable bulbs and the characters of the flowers is so highly developed that the Dutch bulb-grower Voorhelm is said to have been able to distinguish more than a thousand varieties of hyacinths solely by inspecting their bulbs.

Another instance may still be added. It relates to the association of the color in the bracts, the foliage, and the flowers in the flowering currant (Ribes sanguineum). This

species, of which a number of types are growing on the hills of California, is a very common shrub in European gardens. It has produced a variety with whitish flowers, which, however, still betray their origin by a pale red hue. From time to time it returns to the parent type in the way of bud-variation, producing branches with dark red flower spikes. If now we compare such a branch with the remainder of the shrub, we find that the difference is not limited to the flowers. Quite on the contrary, it shows itself also in the bracts and even in the stalks of the leaves. The bracts are reddish when the flowers are bright, and almost colorless when the spikes are to become white. At the first opening of the buds the color of the flowers may be predicted by this means for each spike of the variable shrub.

Before leaving the correlations of organs in regard to their color, I wish to point out another side of the question, which may throw some light on the intimate nature of correlative changes. The anthocyanin dye is assumed to be, in its chemical composition, related to the large group of tannins, of which the common tannic acid is the best known instance. Hence we may suppose the existence of correlations between the color and the taste, or, going one step further, between the color of the flower and the taste of the fruit or seeds, since tannins may give a peculiar, disagreeable, astringent taste, as is well known in the case of many unripe fruits.

Such associations from time to time occur. As an instance I may quote a variety of the Windsor beans (Vicia Faba), newly introduced by the Dutch seed merchant Van Namen, in Holland, from which the black patches on the wings of the flowers are absent. Correspondingly the young seeds, at the period when they are best for canning, are of a paler color and a sweeter taste than the ordinary sort. This sweetness is caused by the absence of the tannin in

Fig. 76. The laciniate bramble (*Rubus fruticosus laciniatus*) with divided petals. B. A flower of the ordinary bramble.

their coats. By this means the improved variety may be distinguished by the marks of the flowers.

Besides their color, the foliage and the flowers may be correlated in their form. The most striking instance is that of those varieties which have laciniate leaves and repeat the same character in their petals. Two notable plants give proof of this assertion. One of them is the laciniate form of the ordinary celandine, and the other a variety of the common bramble. Its petals are divided into three equal lobes, which in their turn may show small incisions at their top. These are evidently analogous to the repeated divisions of the lobes of the leaves.

All the cases hitherto given were related to homologies between flowers and other organs. But even within the flowers correlations may be observed. They are of numerous patterns, but I must limit myself to one instance. As such I choose the size of the flowers and the relative length of the style and the stamens.

It is a fact of daily observation that many small flowers do not need the help of insects for their fertilization. In a large number of cases their stamens directly touch the stigma, and the pollen is spread over it by the very act of the opening of the anthers. Many of our common species of the large family of the cruciferous plants give instances of this. On the other hand, great size in flowers is often combined with the production of stigma and anthers at such a distance that the pollen can only reach the first by the aid of bees and other visitors.

In the evening primroses, as in many other plants, the size of the flowers depends upon the season in which they open. This dependence may go so far as to change the whole biological aspect of the flower. In the ordinary sorts of the evening primroses (Œnothera biennis and allies), the style is short and the anthers are arranged around the stigma.

Fig. 77. A. Ordinary celandine (*Chelidonium majus*). B. Laciniate celandine (C. *m. laciniatum*), which originated from A in a garden at Heidelberg about 1590. *a* and *b*. Flowers of A and B.

They open half a day before the petals expand the flowers and invite the insects to a visit. During these last hours, within the closed bud fertilization usually takes place, and all is over before the insects come, insuring in this way a

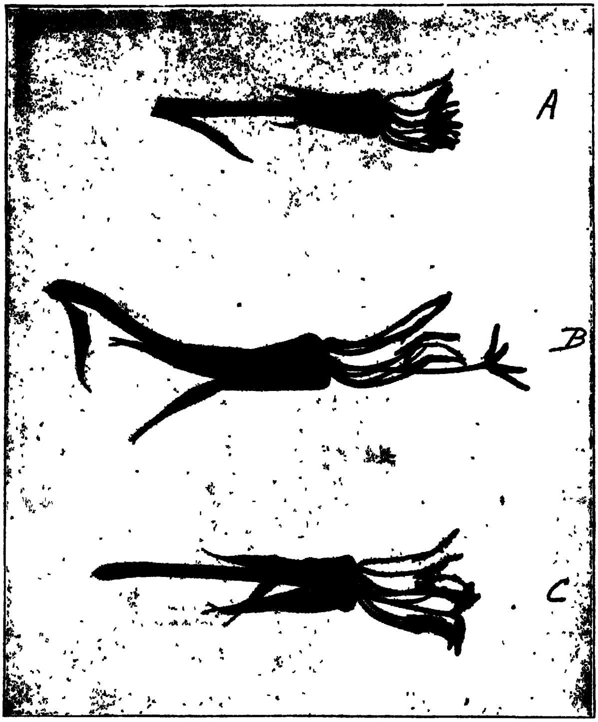

Fig. 78. Flowers of Evening Primroses, deprived of the petals. A. The ordinary species, (*Oen. biennis*), a self-pollinating species, collected near Chicago. B. Summer-flower of Lamarck's Evening Primrose, the stigma protruded beyond the anthers. C. A late flower of the same plant with the anthers touching the stigma.

most complete self-fertilization. Often I have seen the buds drop off before opening without the least detriment to the ripening of the fruit. In other cases I succeeded in cutting away the buds about an hour before their time for opening, but the young fruits had already been fertilized

and they ripened quite in the ordinary way. All the bright display of broad and shining petals, of honey, and a sweet fragrance is here absolutely useless and superfluous. Moths and bees are attracted in large numbers, but the pollen which they bring to the pistils is of no use at all.

The evening primrose of Lamarck widely surpasses its congeners in the size of its flowers. In connection with this difference it produces styles of such a length that the stigmas are elevated above the anthers and cannot directly be touched by their pollen. Here no fecundation is possible without the aid of the insects, and if these are experimentally excluded the flowers fade away without making fruit. All the beautiful and ingenious means of attracting insects come into play in this case. No part of the flower is superfluous, as it is in the ordinary species.

The correlation between size and need of insect aid, however, shows itself as soon as the season draws to its close, or rather as the spikes increase in length. Towards autumn the flowers become steadily smaller and their styles do so too, but in a greater degree. The elevation of the stigmas above the anthers decreases, and in September and October they are touched by the pollen, insuring by this means self-fertilization without other aid. The depositing of the pollen on the stigma is at first only slight and insufficient, but as the summer declines it steadily becomes more complete, and in the end the small flowers at the tops of the spikes are as sure to fertilize themselves as are the brightest blossoms of the Œn. biennis.

If now we compare this case of correlation with the previously mentioned ones, we see that here we have a dependence on external influences, which causes the correlation to come into play, whilst in the other instances no such excitement was required. Hence we see that all correlations are not of the same nature. Some are the result of

the inner qualities or characters of the plant, but others are the product of reactions to external stimuli.

The difference observed in these cases may be considered from a broader point of view. Some cases of correlation are caused by characters which may become active in more than one organ of the plant. The faculty of producing the anthocyanin dye may display itself in flowers, fruits, and seeds, in stems and stalks, in leaves and scales, in one word, in almost all the organs of the plant. It is evidently everywhere the same character, even where it sweetens the taste, by lessening the amount of tannin. So it is with the laciniation, which may affect leaves and petals. In all these cases the idea of unit-characters is pressed upon us. It is the assumption that the same unit becomes active in the different parts of the same organism.

In the other cases different qualities may depend in the same manner upon the changes of the environmental conditions of life. If these are favorable all will increase, but under adverse influences they will decrease together. In this way different unit-characters may be correlated but the relation is more in the nature of accidental coincidence than of actual identity.

All in all, the study of these correlations is of the highest interest, as well for science as for practice. By means of them we may predict one quality or one function from the study of others. Insignificant characters or organs may show us the way and guide us in our selection. The more we familiarize ourselves with such seemingly subordinate marks, and with their relation to the qualities, which determine the commercial worth of the plant or of the harvest, the better we shall be prepared for the work of selection. To judge quinces from their seedlings, as Burbank did, may seem incredible to those who are not initiated into the mystery of this principle, but it can be learned, either

in practice or on the basis of our general conceptions of association of characters.

B. CORRELATIONS IN AGRICULTURAL BREEDING

It seems hardly necessary to repeat the evidence given in the former chapter. We may at once go into the details and consider those cases, in which the correlations give direct indications of valuable qualities to the agricultural breeder. Of course the application of the principle of correlation to the practice of selection means the judging of the worth of single plants on the ground of seemingly insignificant marks.

As a first instance I choose the peas, which have been studied from this point of view by Tedin. Peas, as they are commonly cultivated, are considered as belonging to two nearly allied botanical species, Pisum arvense and Pisum sativum. In reality they consist of numerous elementary species, which are quite distinct from one another. More than a hundred types may be distinguished by the color of the flowers and of the seeds, by the number of the kernels in the pod, by the disposition of the flowers along the axis, whether solitary or placed in pairs, by the character of the ramification of the stem, and by numerous other subordinate marks. Each of these qualities proves to be constant in pure cultures, and each is correlated to some feature which may be of influence on the harvest. Among them the time of the beginning of the flowering period is related to the period of the ripening of the seeds in so simple a way, that it may easily be understood, and that we only wonder how it has been possible that it has not previously been discovered. Some individual plants produce their first flower in the axil of one of the lower leaves of the stem, but others are bare of flowers over a notable length. Now it would seem that this was only a case of fluctuating variability, the length of time

required for the beginning of the blooming period varying in the different individuals. If this were so, the character would only be of slight value, and, in the main, dependent on manure and culture. But Tedin found that there are a number of types, differing from each other in the age in which they begin to flower, and that each is constant, when propagated from pure seed. Moreover he observed that the early-flowering plants are early in ripening their seeds too, while the late-flowering individuals bring their harvest only in the latter part of the season. That this would hold good for the first pods, might be expected, but the observation showed that the rule is applicable to the whole harvest.

Earliness of ripening often is a most prevailing point in the determination of the cultural worth of a variety. The influence of unfavorable weather, such as often occurs in the latter part of the summer, is thereby eliminated. Heavy rains may bring the necessity of harvesting in a moist condition. Warm and damp weather without sunshine may induce the plants to produce a rich foliage consuming the nutriment for the pods and thus deteriorating them. Cold days protract the process of ripening and thus prolong the exposure to insect pests. All kinds of dangers speak in favor of the cultivation of early varieties.

Such may now be secured by the correlated mark of the place of the first flower on the stem. On the ground of this mark promising plants are selected and isolated in order to determine their worth afterwards, in their own harvest and in that of their progeny.

Apples and pears may give a second instance. In the first half of the last century the Belgian horticulturist Van Mons discovered the significance of their numerous elementary species and the relation between their fruits and the form and growth of their foliage and branching. Since his time much has been done for the amelioration of these im-

portant trees, and numberless new varieties have been produced. Among them, more than once it has been the aim of the breeder to obtain seedless fruits, and shortly after the time of Van Mons some such types have been propagated and introduced into trade, but without any noticeable success. In European gardens, here and there, and not even rarely, some old tree is still testifying of these attempts. They belong to more than one variety, as for instance the "Bergamotte sans pepins" and "Riha's Kernlose Butterbirne." But as yet no breeder has succeeded in combining the lack of seeds with other desirable qualities. Of late, in America, the Spencer Seedless Apple Company at Grand Junction, Colorado, promises to introduce a new and better seedless variety of apples.

Now the lack of seeds is directly correlated with some other valuable qualities. In the first place not only the kernels are absent, but also the core, and the whole heart of the fruit consists of succulent and eatable tissue. No labor has to be spent in boring out the core, when preparing the apples for conservation, and no useless parts heighten the freight in shipping. These, however, are not the most important qualities of seedless fruits. Quite on the contrary, the relation of the seeds to the nourishment of the tree is preponderating. The seeds contain the germ of a new tree, and the nutriment necessary for its first development. For a large part this consists of albuminous substances and their production exhausts the tree to a much higher degree than the many times more voluminous, but only sugary tissues of the whole apple. Seedless trees, therefore, are much less exhausted by their fruits than ordinary varieties. Their harvest will be larger with the same consumption of manure or with the same extension of the foliage and roots, which absorb the nourishment and prepare and send it to the fruit. Experience has shown the high significance of this relation

for the oranges of southern California and many other kinds of fruit-trees, and we may confidently assume that the same rule will prevail for all other trees.

Among agricultural plants instances of observed correlations are very numerous. In potatoes richness of flowers indicates a late ripening of the tubers, an abundance of seed-berries is related to a smaller production of potatoes, and in the same way the extension of the foliage, the number, height and branching of the stems and some other marks may be used in predicting the qualities of the harvest. Flax may be judged by its stalks. Long and thick stems, numerous side-branches, and numerous pods are assumed to be indicative of strong development and long and solid fibers. In hops the late kinds are richer in resinous substances, but their aroma is not so fine as in the earlier sorts and the botanical marks of the hop-bells, such as hairiness, length of the axis between the succeeding bracts, and many others may be made use of in judging the value of the different varieties. Clovers are very rich in elementary species, which may be discerned by the form of the leaves, by the presence or absence of whitish spots on the leaflets, by the size and the color of the seeds and by some other marks, correlated with the practical qualities of the types under consideration. Varieties of vetches (Vicia) in which the stems begin to branch at a short distance from the root are less sensible to frosts and bad weather during winter than those which remain unbranched for a longer period. Numerous other instances could be given, showing the interest attached to a thorough study of apparently insignificant marks and even of such differentiations as escape the attention of the ordinary observer.

Instead of prolonging the list, however, I prefer to call attention to some cases of especial interest, in which the correlations may be more or less clearly understood. One

of the most prominent features in the value of agricultural products is found in the size of the seeds, or as it is often stated, in the number of seeds wanted to fill a liter. Larger seeds are as a rule preferred, and many regions which are renowned all over the world for the superiority of their seed grains, owe this repute in a high degree to their care in sifting the seeds and separating the biggest ones as well for the continuance of their race as for sale. It is interesting to look into the reasons for this preferment. In the first place comes the relation between the useless and the useful parts of each single kernel. In a seed the inner or nutritious tissues are surrounded and protected by the outer layers or integuments. The inner parts may consist of the germ alone, or of the germ and the albumen, the germ containing chiefly the albuminous and oily substances, and the albumen being ordinarily the tissue in which the starch is the most prominent nutritive element. The integuments or outer layers are not only devoid of nutritious contents, but are also ordinarily of a considerable firmness. They are built up of different tissues. In the seeds of the clover the external layer is cuticularized. These coverings have their significance for the protection of the germ against all kinds of dangers, but considered in the harvest they evidently diminish the quantity of nutrient parts per unit of weight. Hence the conclusion that the nourishing value of a given quantity of corn, of grain, of peas, or of any other eatable kind of seed, depends in a high degree on the development of those integuments. The thicker they are, the less is the part of the useful tissues, while seeds with thinner shells contain more nutritive parts, and moreover are more easily digestible.

Therefore the breeder always has to select the plants with thinly covered seeds, and the correlation which exists between this quality and the size of the seeds is his easiest

and most reliable guide. For numerous determinations have taught that large seeds have thinner integuments than smaller ones. This rule holds good for grains and peas and probably for all agricultural crops, and even for flowers and wild plants the same relations prevail. The size of the germ and albumen and the development of the surrounding layers are evidently dependent on the same influences. Individual strength of the variety, or a better nourishment of the single plants will cause both of them to increase. But the measure of the increment will be different for them, and therefore their proportion in weight and volume will be affected by the change. The relation is the same as that which we have studied in our last chapter for the size of the flowers and the length of the styles in the evening primroses. Or, in other words, favorable conditions will promote the development of the inner nutritive parts of the seeds in a higher measure than that of the less digestible coverings. The preference commonly given to large seeds may be explained by the evidence afforded. But the detailed correlation is not the only one. On the contrary, the size of the seed is correlated with its development during the germinating period, and, through this, has an influence on the individual strength and size of the whole plant. Moreover, larger seeds are known to be more equal in size, the smaller specimens which are so common in non-selected samples, failing in them. This conformity results in simultaneousness of germination and development, two of the weightiest factors for a regular growth of the crop. Especially they determine whether at the time of the harvest all ears or all pods will be duly ripe, or whether a larger or smaller part of them will be lost. Ripening too early, an ear may lose its kernels before the harvest, whilst ripening too late it is of no use at all. A simultaneous development, therefore, is one of the most desirable qualities in cultivated plants, and this may be

reached by selecting on the ground of seeds of equal size, or simply on the base of choosing the largest seeds. Apart from these general correlations there are two minor points, for which I might call your attention. The first is indicated by the common proverb:

One year's seed
Is seven years' weed.

It means, that a large number of weeds and other wild plants produce seeds, only a part of which will germinate in the next spring. Another part will sleep in the soil and only be awakened in the spring of the following year, whilst the more resistant kernels will stand two or more years and come into germination after this prolonged period of rest. Some spare seeds may even rest as long as six or seven years; whence the saying quoted. This rule is not at all limited to weeds, but embraces the different sorts of clover and of other allied leguminous forage plants.

Now, here also, we observe a correlation between the size of the seeds and the time required for their germination. As a rule, the smaller seeds have the thickest and hardest coats, as we have already seen, and it is exactly the extreme resistance of the coats, which causes them to lie dormant for so long a time. If we sow seeds of common clover or of the crimson species (Trifolium incarnatum) on a layer of moist blotting paper, we can easily pick out day after day those which produce their rootlet. In the main the larger seeds will thus be seen to germinate first, and after a week or more only the small kernels remain. Among these, some will germinate during the next weeks, but some spare ones will remain dormant until the next year.

Evidently it is of high practical interest, in the first place, to have all or nearly all the seeds of a sowing germinating in the same spring, and in the second place to have them all coming up in the same week or at least as nearly at the same

time as possible. Varieties with larger seeds are therefore preferable by far, since they do not contain the aberrant little ones, which are the chief cause of the loss and of the trouble.

At the Swedish agricultural experiment station at Svalöf another method has been developed to get rid of this nuisance. Though it is not directly related to our main subject, it is as well to dwell upon it here, for a short time. It has been discovered that with clover and other leguminous forage crops the whole question of the sluggishness of the germinating process is due to the resistance of the outermost layer of the seed coats to the absorption of water. Small seeds of clover remain absolutely dry in water for days and weeks, and in this condition they may even be thrown into boiling water without being killed. It is the very thin cuticle of their epidermis which impedes the penetrating of the water into the inner parts and thus prevents the initiation of that process of saturation which is the necessary condition of all germination. If there were only a small hole, or a small non-resistant spot, the water might pass by this and effect a complete imbibition. On this principle the Svalöf method is based. It allows of filing all the seeds on a small spot, making their coats locally permeable for water, without changing them in any other way. In order to do this, an apparatus has been built, which throws the seed against a filing disk in an oblique direction and in continuous current. Thereby the culture of many species of leguminous plants has been made possible and advantageous, which formerly were disregarded on account of their imperfect germination. By this means the selection of larger seeds and the application of this part of the principle of correlation is made superfluous.

My second point is the value of rapidly germinating seeds in all cases where the germination period is the time

Fig. 79. Panicles of oats. A. With erect, and B. With spreading branches.

for the attacks of some dreaded disease. For the sooner the time of sensibility is over, the smaller will be the harm and the larger the number of uninjured thriving plants. Experiments have been made in this direction in Sweden on the resistance of grains against the devastations of the frit-fly (Oscinis frit). This is a little black insect, attaining a length of only 2 or 3 mm. and easily recognizable by its metallic brightness, black legs, and yellow feet. It invades the grains chiefly during the germination period, depositing its eggs on the young plants. The larvæ creep along the leaves and their sheaths downward until they reach the young halms, and in eating these they destroy the germ of all further development. Some of the seedlings may die shortly afterwards, others may show signs of life during some time, but their growth is abnormal and for the harvest they are wholly lost. Whole fields of all kinds of cereals may be destroyed by this calamity during some few weeks.

One of the best means against the attack of these flies is the passing of the dangerous period of life as rapidly as possible. As soon as the young halms are old enough to resist the invasion, the insects become nearly harmless. On the basis of our considerations concerning the correlation of the size of the seeds with the rapidity and simultaneousness of the germination, we may therefore expect that the sowing of selected large seeds or of large-seeded varieties will give the desired protection. This is exactly the result of the Swedish experiments. Nilsson and his staff made comparative sowings of large and of small seeds separated from one another by sifting, or even by simply choosing the upper kernels of each spikelet for one trial, and the under kernels, which as a rule are larger, for the other. By this method all varietal differences were excluded and the result was for oats, that the loss from the attacks of the fly was small for the large seeds, but very notable among the smaller,

and therefore more slowly and more irregularly germinating kernels.

As we have already seen, correlations may be divided into those, which are easily traceable to a common cause, and those in which the causal relation of the single phenomena remains obscure. In the adduced example of the seeds this relation is evident, at least to some extent, and therefore I will now choose a case in which there is no obvious reason for the connected qualities to be so connected. Our appreciation of the correlation can in such cases only be based on direct observation. This however, requires a most minute study, on one side of seemingly insignificant botanical characters, and on the other of the industrial qualities of the plant.

Among the grains the panicles of the oats give the best evidence. Their shape and mode of branching are variable to a high degree. The branches are combined into whorls. The number and relative development of these branches proves to be constant for each pure type. The apparent high variability is to be reduced to a large group of single forms, which when considered for themselves are narrowly circumscribed and do not transgress their differentiating limits. Some panicles have their largest branches longer than the main axis, in others they are shorter. Those of the first group are ordinarily stiff and dense, those of the second being more flaccid and more widely spread. The biggest kernels may be found in the lower spikelets, or they may prefer the middle and upper ones, and experience has shown that only such sorts are commendable which have their biggest seeds above the middle.

Most reliable marks are given by the color of the seeds. The slightest differences in tint are wholly constant and indicative of corresponding practical qualities of the sorts. Yellow and yellowish, straw and reddish-yellow, whitish and

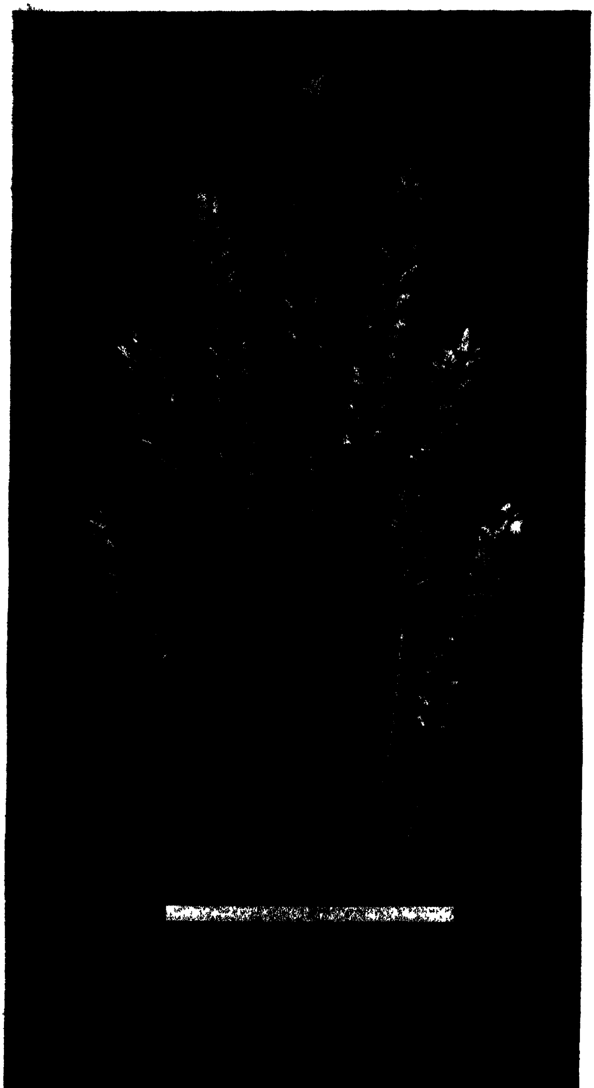

Fig. 80. Svalöf Grenadier wheat, the best of the new Swedish varieties of wheat, very productive of grain and straw.

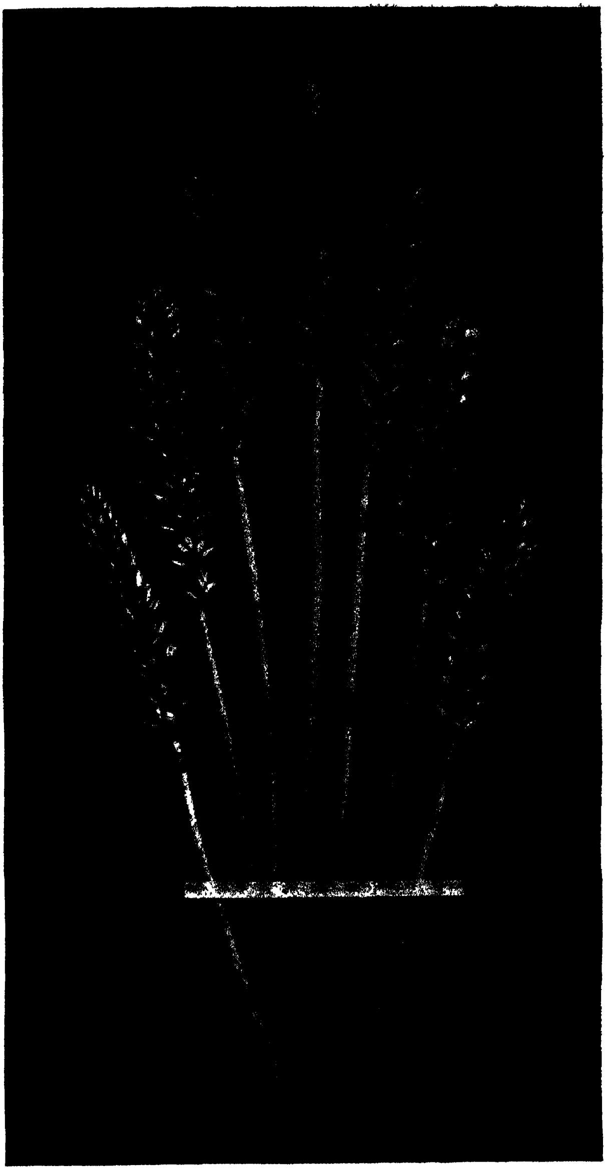

Fig. 81. Svalöf Bore-wheat, a new hardy variety for the cultures of middle Sweden.

grayish-yellow tinges, half a dozen of shades of brown, and more of less completely black types may be distinguished. Some of them have given proof of being suitable for some regions and some uses, while others are preferable under other conditions.

The spikelets may contain one, two, or three flowers, and these numbers are dispersed on the different branches of the panicle according to the special properties of the sorts under consideration. Spikelets with two flowers are as a rule preferable, since there is a near relation between this number and the size of the kernels. In each spikelet the flower of the undermost palet always gives the biggest kernel. If it is the only one it may be small, but as soon as it becomes accompanied by a second or a third flowering scale, its kernel becomes heavier. In this way the many-flowered spikelets do not only give more kernels but also bigger ones, and with them all the advantages we have described of large seeds. The size of the empty scales at the top of the axis of the spikelet, the little hairs at the base of the palets, the more or less twisted awns and their curvature give many morphological marks, whose correlation with the breeding qualities may be studied.

Corresponding marks are afforded by wheat, and rye, and barley. Among them the number of the kernels in each spikelet prevails, but the size and density of the whole ear, the characters of the outer scales, and even their hairiness may be advantageously compared. At the Swedish agricultural experiment station, for each genus of cereals a system of classification has been traced which gives a survey over all these botanical marks and their relation to industrial qualities. These relations of course have had to be studied experimentally, and large cultures as well as exact measurements and determinations of chemical value, baking and brewing qualities and many others have been made. It

has taken years to arrive at a sufficient degree of knowledge of all these correlations, and the investigations, though covering more than ten years, have as yet not nearly been exhausted. But the general result has been that the industrial worth of any individual plant can now be estimated by a thorough inspection of its panicles or ears and with a degree of certainty which is wholly sufficient for all purposes of selection.

As an illustration of the high significance of these correlations, I will now return to the example of the Primus-barley, of which I spoke in a previous lecture. As already pointed out, all endeavors to breed a race of Chevalier-barley with stiff culms had led to no appreciable amelioration, and the cultures in this direction had to be given up. The principle of correlation, however, pointed to another way of solving the problem. Instead of trying to breed a Chevalier-barley with rigid halms, a stiff variety was chosen, and it was proposed to give to this the qualities of a fine brewer's barley. In Sweden a kind of barley is largely cultivated which bears the name of Imperial barley and belongs to the subspecies of Hordeum erectum with stiff culms, hairy scales, and coarse kernels. This variety, the good qualities of which were duly appreciated, was taken for a starting-point in order to produce the desired barley for the brewers. The study of the correlations between morphological and industrial features had led to the discovery of a coincidence of some marks of the hairs on the base of the scales with the composition of the albumen of the grains. Long and straight ones are correlated with coarse kernels, but short and crisp, more or less woolly hairs are indicative of those qualities which stamp a barley as a good kind for the brewery.

On the basis of this correlation, combined with the discovery of the existence of innumerable individual variations, it

was judged probable that among the resistant Imperial barley some spare individuals might be found with compact kernels, suitable for brewery purposes, and that they would be recognizable by the form of the hairs of their scales. This conclusion led to a formal hunt for such specimens. Of course, among some hundreds they could hardly be expected, but in each thousand it might be possible to find a single one. All the fields of the Imperial barley of the station were scrupulously inspected, and any specimen with a diverging type of hairiness was marked out. Many thousands of plants with long and straight hairs had to be analyzed before the desired ones could be found. At the end some sixty were judged worthy of further trial. Their ears were collected separately, and in the next season the progeny of each single selected mother plant could be studied. The investigation was now directly turned to the brewery qualities and taught that in some thirty of the cultures the expected correlation was really present.

This result crowned the labor of the previous summer, as well as it gave proof of the reliability of the principle involved. It was quite sufficient for the practical aim of the experiment. On the field plots of this second generation eight new and valuable types could be discerned, each of them evidently a fine brewer's barley with resistant halms. They were quite as good as the ordinary cultivated Chevalier sorts, though not at all derived from them. Among them all further care had to be directed to a rapid propagation, and to comparative trials of the eight élite strains. One of them was found to be the best, and to comply with all the demands of the brewers. It got the name of Primus-barley, as already quoted. It was resistant even on the hardest soils of Middle Sweden, but its kernels can scarcely be distinguished from those of the best Chevalier varieties. It is a brewery barley of the very first rank, on account of its

pale yellow color, its smooth and downy coat, its typical form, and the chemical qualities of its tissues.

This new race has been constant and uniform from the very first moment of the discovery of its mother plant. Its progeny had only to be multiplied, absolutely no selection being wanted. The multiplication has been very rapid, and nine years after its commencement (1892) it could be given into trade (1901), having triumphed at numerous agricultural expositions over all other similar sorts.

Apart from the enormous amount of work involved, as well in the selection of the first year as in the consecutive comparative trials of the originally isolated strains, this great success is in the main due to the discovery of the laws of variability and correlation governing the characters of our cereals. It is a principle, which already has given proof of its wide applicability to nearly all the large agricultural crops, embracing even the minor types, such as vetches and other leguminous forage plants. It is a leading idea, and hardly any limits seem to be set to its influence. To the practical breeder it shows the way in nearly all the burning questions, and for the scientist it may prove to give the solution of numerous problems which have eluded his evolutionary speculations for more than half a century.

C. A METHODICAL STUDY OF CORRELATIONS

Correlations between botanical marks and breeding qualities are to be considered as reliable guides in the work of selection. Numerous instances have been dealt with in which single individuals, chosen in a field on account of some slight deviation of form, color, or hairiness, have become the parents of valuable varieties. Until some years ago our knowledge of these correlations was limited to a greater or lesser number of isolated cases, and although their significance was clear enough, it was hardly possible

to point out the way in which further progress might be attained.

At the Swedish agricultural experiment station of Svalöf, however, it soon became evident, that this principle might some day become the basis of exact methodical work. The fact once ascertained, that the fields of our ordinary crops are by no means uniform, and moreover conceal a noticeable number of excellent types, suitable for the most widely different requirements, the need was instantly felt for a method which would enable the breeder to make his selections as large and as profitable as possible. According to the rules already explained, this choice must always be a two-fold one. In the first place comes the work in the ordinary fields, the picking out of the aberrant individuals which seem to promise some special result. Thousands of ears are inspected and tested, and on account of certain marks those are chosen which do not comply with the main type. Then their seeds are sown, and the progeny of each single specimen is studied and compared with the already cultivated varieties. This comparison depends in part on the same marks as the initial choice and in part on the direct control of the agricultural qualities. By means of this latter the judgment is finally made independent of the laws of correlation, which by this contrivance afford only the means to reach the aim by a far shorter and easier way than would be possible if the first choice itself had to be made on the basis of exact measurements of the practical value of the individual plants.

We thus see that we may limit our study to the initial choice. We may leave the subsequent work out of consideration, since, as far as the correlations are concerned, they require the appreciation of quite the same marks. But in order to make the first choice as reliable and as profitable as possible, a thorough knowledge is required. It must

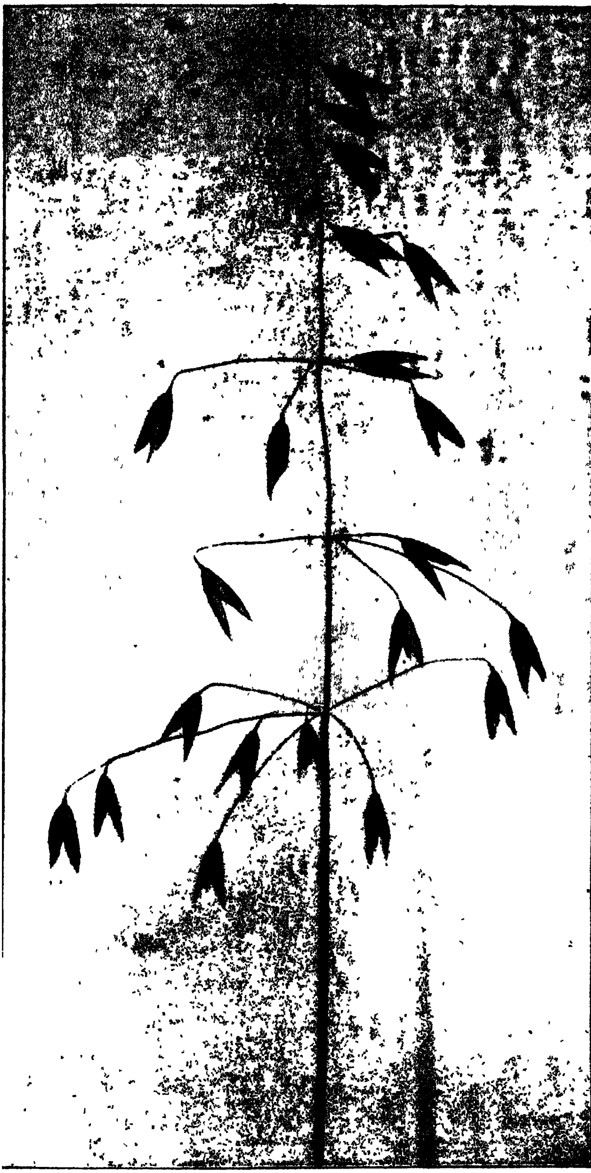

Fig. 82. A panicle of oats with weak branches, photographed at Svalöf, Sweden.

include three subdivisions. These have to deal respectively with the morphological marks, with the agricultural qualities, and with the correlations between these two groups. The agricultural qualities may be assumed to be manifest, but the botanical peculiarities have hitherto been neglected, or studied only in a superficial way, so far as their appreciation was needed for the ordinary botanical systems.

These older systems were based on a very imperfect knowledge of the real nature of the variability. No sowings had been made in order to study this phenomenon, and it was simply assumed that all minor peculiarities, in which the single individuals of a species differed from one another, were changeable and did change from one generation to the next. On this assumption their intricate nature could hardly be of any significance for the systematist, and was therefore almost always neglected.

The discovery of the numerous elementary species, of which the common varieties consist, has at once changed the whole aspect of this question. Numerous apparently insignificant marks proved constant in pure sowings. They offered an easy and reliable means of distinguishing strains of widely divergent practical value. Thence the conclusion that they must be subjected to an exact study, which would enable the breeder to discover any new and useful type that might occur in his fields.

In order to do this, a thorough study had to be carried on for a number of years. The single characters had to be classified, so as to give distinct systems. In these, each botanical mark may be indicated in combination with its correlative significance. By this means, whenever a distinct practical quality is wanted, the correlated botanical marks may be looked up in the system.

Such elaborate systematic surveys have been published from time to time by the experimenters of the staff of Svalöf.

Fig. 83. A panicle of oats with stiff branches, photographed at Svalöf, Sweden.

They include the cereals, the peas, some leguminous forage crops, and a small number of other agricultural plants. As an instance, I choose the system of the wheat. It embraces seven divisions, which are indicated by the name of types. They are distinguished by the qualities of the ear which may be long or short, tight or brittle, and densely or loosely covered by the spikelets. In the first place comes the widely known type of the Squarehead with its butt-ended ears. From this are derived varieties with ovate ears, whose broadest part is seen in the middle. Cylindrical ears are of the same breadth throughout their whole length, but in one type they are almost square and in another more or less flattened.

These types are further subdivided, according to other marks, each of them embracing some four or five groups of minor value. They are distinguished by the color, size and form of the grains, the marks of the scales, the occurrence or absence of awns and other similar marks. All these seemingly insignificant characters have been shown to be constant in the pedigree cultures, and an exact study of them enables the breeder to recognize each single type. So it is also with the minor marks, by which the single kinds are finally distinguished. Often these are almost invisible to the inexperienced eye, and years of persevering study are necessary to obtain the faculty of recognizing them easily and rapidly.

With this object in view a division of labor has been established, finely adjusted instruments for measurements and comparison have been invented, and large collections of samples and pictures have been brought together. Each of these points now demands our special attention.

Division of labor has been the first requirement, the study being so extensive that it was impossible to take more than one agricultural species into consideration at a time. The panicle of the oats, which was described in our last

chapter, afforded the most promising instance, and was studied first. Soon afterward other cereals and peas were treated in the same manner, then vetches, but most of the other agricultural crops have been taken into consideration only during the most recent years, or are still awaiting attention. Gradually many hundreds of definite forms were distinguished within each species, and the amount of work became so large that it was necessary to divide the subject among several investigators. Neither the time nor the memory of one man was sufficient to embrace the whole realm of the botanical marks and of their correlations to breeding qualities for all the elementary forms of more than one or two species. And perhaps just this statement is the best way in which to convey to the layman an idea of the enormous amount of work that is involved in this study, and required for the complete exploration of all the single forms, now growing mingled together in the fields.

At Svalöf the director Dr. Nilsson has chosen for his own department, the cereals and especially the oats, and is assisted in this work by Mr. Nilsson-Ehle. The leguminous crops, such as peas and vetches, are the department of Dr. Tedin. Rye has been studied by Mr. Wallden and potatoes by Mr. Lundberg. Other special crops have been given into the hands of Mr. Elofson and Mr. Witt. Each of them has become a specialist in his line and has acquired a high degree of ability in singling out the rare promising individuals from among the thousands of ordinary specimens, which commonly constitute the majority of the ordinary varieties. An instance of this work was described in our last chapter, in the production of a brewer's barley with stiff culms. By such means it becomes possible to estimate the probable agricultural value of all aberrant individuals. Whenever a distinct quality is desired, either in order to improve a local variety, or to bring it into a form suited for

other conditions of soil or climate, or to comply with any other wishes of agricultural practice, it is necessary only to know the botanical marks correlated with the desired qualities. On this basis individual plants may be singled out, and after multiplication through a few years, their progeny will probably respond to the demands made, as soon as the industrial qualities themselves are investigated.

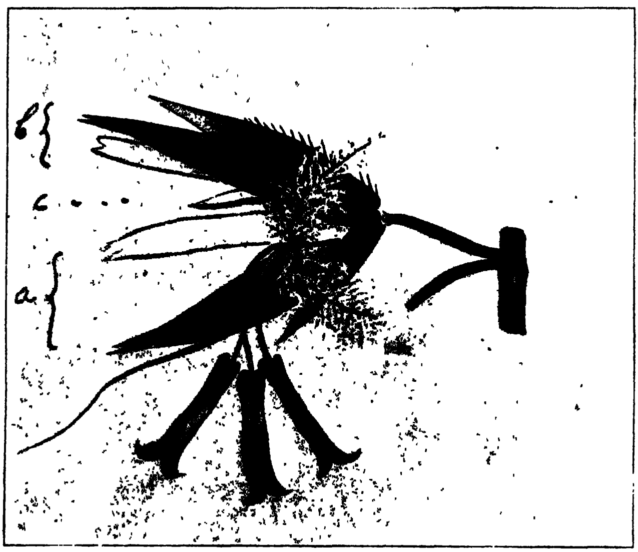

Fig. 84. A. Spikelet of oat-grass (*Avena elatior*), showing a flower with two palets, three stamens, and two stigmas (a), a flower bud (b), of which only the palets are visible and the third or sterile flower (c).

Some instances of correlations may now be presented. Different elementary species of oats are distinguished by the form of their panicles. Some are stiff with a firm principal axis and erect branches. In others the axis is weak and the branches droop. In some varieties they are widely spread, but in others they all bend to one side. According to these marks definite types have been distinguished, and in com-

paring these with the industrial value of the varieties it has been discovered that stiff and erect main branches building a dense tip on the panicle are indicative of the richest harvest and of the best kind of kernels. Varieties with loose flexuous branches are usually only poor yielders. The

Fig. 85. Barley. A. A complete spikelet with the three flowers. B and C. Single flowers seen from different sides, showing two palets, three stamens, and the ovary with the stigmas. In B also the two outer scales or glumæ with the stigmas. D. Stamens and ovary of a flower.

number of the grains in the single spikelets affords another instance. It is correlated by distinct laws to the size of the kernels, and through this mark to the industrial value of the variety. Moreover these numbers are strictly hereditary and so give very reliable marks. Oats and wheat especially

have been studied from this point of view. In barley, one of the main characters and one which has been already alluded to is found in the hairiness of the scales, bristles, and other parts of the spikelets and flowers. In some cases the hairs are smooth and pressed against the scales, in others they are stiff and spreading. Crisp and woolly hairs are, as a rule, to be considered as indicating the most valuable types. Experience has taught that in this simple way it is possible to select in each variety the elementary form that will probably be the best yielder. The midveins of the outer scales afford still further marks. In some cases they are smooth, in others armed with small but sharp teeth. Even these differences are constant in pure cultures, and indicative of correlated yielding qualities.

The same laws of correlation have been observed with other agricultural plants. Prominent amongst all are the forage crops of the large family of the leguminous plants. Here the differences between the numerous elementary forms within the botanical species are not so very small and so difficult to realize as in the cereals. Peas and vetches have been studied in the first place, but clovers, wild species of sweet-peas, and several other forms, whose culture had as yet hardly been profitable, have also afforded notable results. For peas the correlations have been studied by Mr. Tedin, who has published his results in tables, giving the average weight of the seeds, their number in the pods, and their total number on the individual plants, in combination with other valuable qualities. On the ground of this system he has been able to distinguish 500 different kinds of peas, which have proven constant in his pedigree cultures, and among which some 40 could be selected as evidently excelling the ordinary varieties out of which they had been isolated.

In the same way some 75 new and constant types of

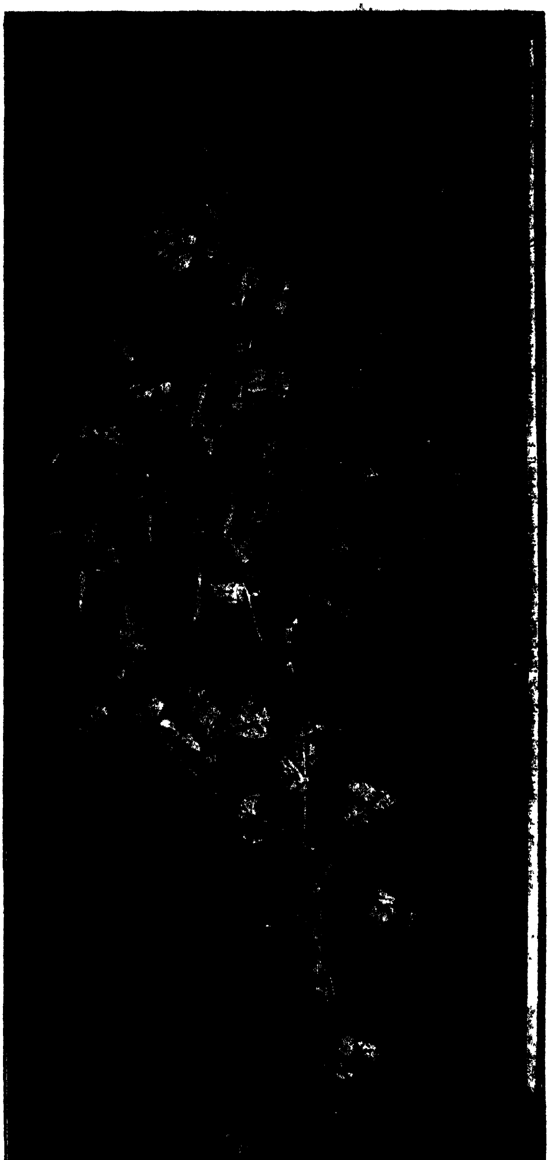

Fig. 86. Svalöf Solo pea, a new forage-plant, most productive of seeds and foliage. Leaves green.

vetches have been isolated at Svalöf. In some of them the flowers are white, in others pink, instead of being purplish, as in the ordinary sorts. The seeds may be spotted or not, of a dark or of a pale hue. The spots are small, isolated, and rounded in some varieties, but in others they radiate from the hilum like tongues of flame. Minor marks are afforded by the size and shape of the leaves, the length and mode of branching of the stems, the distribution of the pods along the branches, and so forth. All these marks are constant, as soon as cultures are made, each starting from a single parent plant. An elaborate system of the vetches has been derived from them, and the single types are now being cultivated separately, in order to examine their industrial value.

Similar investigations have been made for clover. The spanish or red clover was formerly imported into Sweden where the first work has been the controlling of the value of introduced sorts and of their fitness for the Swedish climates. American sorts of clover proved too susceptible to the hardships of the Swedish winters, but many of the kinds of Middle Europe were resistant enough to be cultivated with success. The red clover is very variable, in respect to the shape, and size, and color-designs of its leaves, as well as to the flowers and flowerheads and especially in the colors and qualities of the seeds. A great number of types could easily be isolated. This richness in forms and the constancy of the isolated types had already been studied in several other countries, as, for instance, by Schribaux in Paris, and by Martinet in Geneva, and their different commercial value had clearly been pointed out. But by means of the methodical study of the botanical characters, which is the principle of the work at Svalöf, a far larger number of types could be isolated and varieties be originated which complied with all the divergent demands of the soils and climates through-

Fig. 87. Svalöf Gröp pea, a new early ripening forage-plant.

out Sweden. Similar results have been obtained with the white and the crimson clover.

Many other species of leguminous plants are available for the culture of green fodder. Different kinds of lucerne, of which the alfalfa is the best known species, some forms of Lathyrus, and others have been included in the tests. They are rich in elementary types, but even of the botanical species the agricultural significance was hardly known. Some instances may here be given. Lathyrus heterophyllus is an early ripening species, with sweet tissues and a vigorous growth. It is an excellent yielder. Lathyrus pratensis and Vicia Cracca, two common species along road sides in Europe, recommend themselves by their fitness for mixed cultures on meadows. A richer type of Lotus uliginosus with broader leaves and a resistant variety of Lathyrus sylvestris have been isolated.

Potatoes, beets, and even the ordinary meadow-grasses have been subjected at Svalöf to the same methodical study. It would take too long to give all the details. It may suffice to choose the grasses as a last instance. On meadows, the vegetation is a more or less mixed and motley array of numerous types, belonging partly to the grasses and the leguminous family, partly to other less valuable or even obnoxious species. The value of the different kinds of grasses depends mainly upon the question whether they are at their fullest development at the time when the hay is cut. Some species are too early, become woody, and lose their nutrient qualities before the harvest. Others are too late, and have only produced part of their foliage at that time. Both, of course, constitute a distinct loss, and it must be considered a chief aim in the improvement of meadows to replace them by types which will ripen simultaneously.

Now the experiments at Svalöf, although as yet only few in number, have shown that the ordinary grasses are

Fig. 88. The wild oat-grass (*Avena elatior*), a pasture grass.

at least as rich in elementary species as the cereals. These minor types can be distinguished by botanical marks which are correlated to the time of ripening and to their yielding qualities. Especially variable are the common Avena elatior and the different species of Agrostis. The first of them gave 14 distinct forms in the first trial, and later this number was increased to about 50.

In concluding this hasty survey of the results of the methodical study of correlations at Svalöf, I might emphasize the great principle of the combination of the scientific and the practical sides of the question. Selection on the ground of practically valuable qualities only, has been the rule until very recently. Of course it was a good and reliable method, but it was extremely limited in its application; on the other hand, the whole history of the breeding process in Germany consists of isolated cases. No doubt these have yielded very valuable results, but the Svalöf principle gets rid of the incumbrances to a more universal use. By it the breeder is enabled to single out hundreds of valuable strains, and to select among them the very best. The search in the field is made on the basis of marks which can be recognized instantly by the experienced eye, upon a simple inspection of the ears and panicles, of the stems and their branching, and of the shape and size of the leaves. Thus the purely morphological distinctions take the place of the agricultural tests, which embrace measurements and estimates, that can hardly be made for single individuals and never can be applied to so large numbers of specimens as can be compared by purely scientific marks. A broad scientific foundation is thus seen to be the means of abridging the practical work and this to such a degree that the selection may be extended and applied to almost all the requirements of practice at large.

Two essential features of the selection work at Svalöf

are still to be dealt with. A short description must be given of some of the new instruments for measurement and comparison, and the collections of samples and pictures of selected plants must be mentioned. In the list of apparatus the "classificators" may be described in the first place. This name is given to small collections of say 15 to 40 ears arranged according to a definite character. For each quality a special classificator is at hand, so for instance, for the size, the shape and the density of the ears. In order to classify an ear it is shoved along the row, until it falls between two ears of the classificator, one beyond and the other behind it. The intervals between every two succeeding ears of the apparatus being marked by figures, the figure on which the ear falls is the indicator of its degree of the character in question.

The transparency of the grains of barley is measured by means of screens with holes. These are exactly filled by one grain each, and the standard-kernels are arranged according to the degree of their diaphaneity. The grains to be tested are put into similar holes of a little separate screen, which can be shoved along the classificator until their transparency coincides with that of one of the standard types. The degree of mealiness is tested by a small pincer which measures the pressure required to squeeze the kernels into pieces. Other instruments are so constructed that they collect from an ear or a panicle all the lowest grains, all those of the second rank and so on, in order to determine the average weight of each group separately. As we have seen, the seat of the heaviest kernels is one of the important marks in the testing of varieties of cereals. Many other instruments have been devised in order to make the estimates as independent of personal impressions as possible, and thus to make them thoroughly reliable even if they have been made in different years or in different localities.

From these short descriptions it is easily seen that one of the aims of the method of selection is the grading of all marks in figures. By this means it becomes possible to give extensive comparative surveys of whole groups of newly selected plants or of the strains derived from them and to draw a parallel between the new and the already existing varieties. Without it the testing of the value of many hundreds of new types would evidently be scarcely possible.

With the same object in view larger collections have been made and separate buildings have been erected in order to exhibit them in such a way that they are easily accessible whenever a new form must be compared with the older types. For the testing is by no means limited to the ears and the kernels, but embraces the whole plant, during the several periods of its development. Dried specimens of seedlings must be at hand for all of the useful varieties. The manner in which the culms produce their more or less numerous side halms must be illustrated, also the length and the stiffness of the straw, on which nearly the whole value of some varieties depends. Moreover the varieties are not only to be compared with one another, but their constancy must be tested, and for this purpose some specimens of previous years must be preserved. In this way pedigrees of dry specimens have been built up, which convey to the visitor an idea of the whole previous history of the race, and contain, besides the proofs of its constancy, the indications of any deviation, which may have occurred in it.

These collections are to be considered as living expressions of the systems described before. The investigator visits them with the plant he wishes to classify, and is guided by their arrangement so that he may find the corresponding prototype in the easiest way. They have this great advantage over the printed systems that all the single qualities may be taken into consideration at once, without the labo-

rious comparison of the figures in the tables. It is almost superfluous to mention that the collections are largely illustrated by drawings and photographs, and that charts giving the results of the tables in a statistical way facilitate the work. Pedigrees have been drawn for most of the important novelties of the station.

The work of Dr. Nilsson and his staff at the Swedish agricultural experiment station at Svalöf is a model of the combination of science and practice. The problems it has to solve are purely practical ones, but the method depends upon exact scientific studies. The station is a private enterprise, founded by the Swedish agriculturists for their own direct use; it has neither to serve educational aims, nor to yield results of theoretical significance. No purely scientific researches are carried on, no grouping of results with the sole object of contributing toward the solution of biological problems is allowed. But its experience has taught the indispensableness of scientific principles and methods. Only under their guidance may the practical work be kept within limits which guard it against useless and superfluous experiments, and which cause it to attain its purpose by the shortest and most direct way. This method of applying science to practice has opened previously unsuspected possibilities and discovered new fields of investigation in the study of the highly interesting relations between botanical marks and qualities of practical value. It will soon bear fruit for the doctrine of evolution and for the theory of specific units in addition to its conspicuous results for agricultural practice.

D. CORRELATIONS IN FLUCTUATING VARIABILITY

Correlation is the name given to regular coincidences of apparently independent characters and marks. This regularity is not meant to be absolute; it simply means the more

or less frequent occurrence of the observed combinations. On the other hand the conception does not exclude cases of complete mutual dependency of characters; it is even probable that it embraces many of them, but that our knowledge is still too incomplete to allow us to draw a distinction between these and the ordinary cases. The other extreme in the long list of possible combinations is evidently given by casual and fortuitous coincidences, accidentally repeated in some group of observations. A continued investigation would show these to have no real value, and so they may here be left out of consideration.

After our hasty survey of some of the most interesting facts, we may now proceed to inquire into their causes. These may be brought under two heads. The causes may be internal or external. In other words the correlation may depend on some inner connection of the qualities, or simply on corresponding changes induced by environmental influences. Evidently, the internal correlations are the most interesting, and moreover those which may be the most completely relied upon. Outer life-conditions, working in the same direction on different characters, on the other hand, are more easily understood and more directly accessible for experimental study. On this account a rational treatment will have to begin with the latter, and discuss the former or internal causes of correlation only after the field has been cleared as much as possible of its foreign elements.

For this reason I have chosen for this chapter the study of the influence of external life-conditions on the phenomena of correlation.

Correlated variability is quite an ordinary feature in all plant life. It may be seen almost everywhere. As soon as a plant deviates from its type, it will be disposed to do so in more than one character. This rule holds good for rare and casual abnormalities, as well as for the more normal, so-

Fig. 89 A pitcher-like leaf of tobacco.

called fluctuating deviations from the type. Useful qualities are subjected to it as well as those practically useless marks, which are usually studied merely on account of the valuable indications they so often give for comparative science.

Some of our most convincing arguments may be derived from the study of teratological phenomena. Every one who is collecting monstrosities, knows that they are, to a high degree, dependent on the influence of the environment. Some years are known to be rich, and others poor in abnormal developments. One of the most notable instances is the year 1851, in the summer of which pitcher-like leaves appeared in such large numbers, as to be regarded as a distinct disease. This was the case in the western districts of Belgium, and while roses and other plants were notably affected, the damage done to the tobacco cultures was reported to be quite heavy. In Baden the summer of 1886 and around Paris the fall of 1893 are described as exceptionally rich in abnormal productions, and other instances could easily be given. Evidently some external cause was at work, and high temperature and moisture are among the factors called upon by different authors to explain the fact which so deeply impressed them.

In a single locality the same phenomenon may often be observed. Some hillslopes and some fields are productive of monstrosities, while others are not. By this means a botanist is often enabled to discover the localities, which may give him the deviations he wishes to collect. Sometimes it is one species which offers a profusion of interesting instances; in other cases a more or less large number of plants are included in the phenomenon. This observation is often stated by saying that a monstrosity is seldom seen alone; it is quite generally accompanied by others.

Some instances may be given as proofs. Pitchers are ordinarily built out of one leaf, or of some part of it, but

together with them two-bladed pitchers may not rarely be observed, as in the magnolia and the common plantain. The pelories of the foxgloves are almost always the seat of secondary deviations, such as tube-like petals, fissions of the corolla, multiplication of the stamens, the production of a secondary raceme from within the capsule, and so on. Even

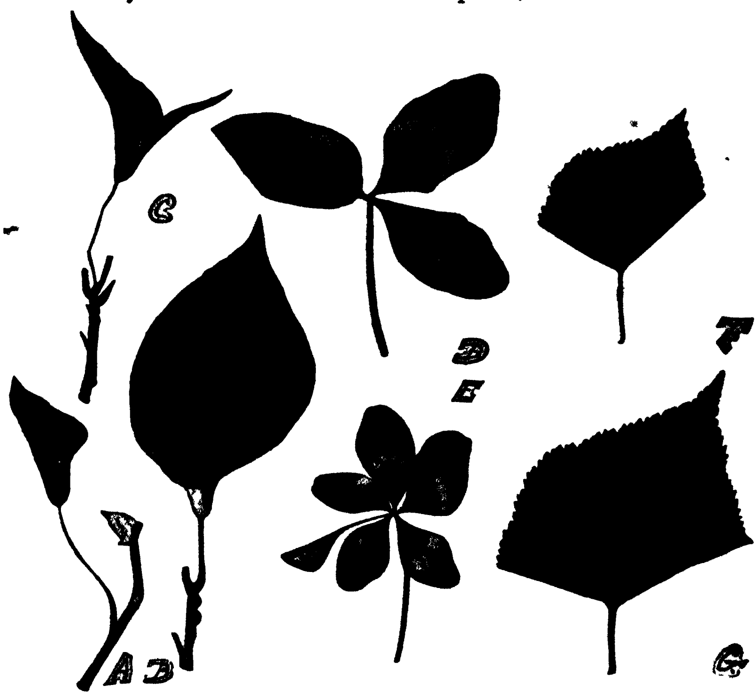

Fig. 90. Pitchers of Magnolia, A, B, C. Of clover, D, E. Of the lime tree (*Tilia*), F, G, One-leaved pitchers. C. Two-leaved. A. Upper part of a leaf only transformed into a pitcher. D, E. Pitcher-like leaflets of the ordinary and of the five-leaved clover.

the beautiful erect peloria of our cultivated Gloxinias often show deviations from the normal number of tips of the corolla and of stamens. Fasciations are usually combined with cleft leaves and other allied monstrosities, and twisted stems are so rich in their deviations as to afford sufficient material for quite a large field in the science of teratology.

On this principle of correlation a definite method of searching for monstrosities has been founded. Years ago I was impressed by the fact that deviations in the seedling plants are often followed by abnormalities in the adult state. By this means, the cotyledons of the seedlings may give indications of what is to be expected. Now it is as easy to inspect thousands of germinating plantlets as it is difficult to cultivate the same number to their full development. But by choosing the stray seedlings with three seed-leaves or with connate cotyledons, the cultures may be effectively reduced, the chance of producing monstrosities on a given space being proportionately increased.

Leaving the abnormal characters, we have now to consider a group of observed cases of correlations in ordinary deviations. I choose my instances from among the agricultural plants. Fruwirth has studied the relations in the development of leguminous crops, at the agricultural station of Hohenheim in Würtemberg. He observed a parallelism between the increase of the total harvest and the weight of the pods, the number and the weight of the seeds. Less intimately, but still clearly correlated with these characters was the average size of the seeds and the average height of the whole plants. Gwallig observed that large kernels are as a rule richer in albuminous substances than small ones. This relation has been found to hold good especially for peas and lupines, both belonging to the same family and often cultivated as forage crops.

Flax has been studied in this respect by Schindler, who stated that the length of the fibers and their total amount are correlated with the total height of the plant, measured from the root to the highest capsule. The thickness of the stem is inversely correlated with its height, higher plants having thinner stems. Therefore, for the harvest of the fibers the thinner specimens and strains should be preferred.

Fig. 91. A. Seedling-plants of Evening Primroses. B. Of the figwort (*Scrophularia nodosa*). C. Of Silene odontipetala. D. Of poppies. E. Of the beech. A 1 and D 1 normal seedlings. A 7, B, C 2, D 4, E, Tricotyledonous seedlings. C 3, D 5, Seedlings with four and D 6 with five seed-leaves. A 2–6, C 1, D 2-3. Different degrees of splitting of seed-leaves.

Tall plants are less branched than smaller ones, and bear a correspondingly smaller number of capsules and of seeds. Potatoes have often been an object for comparative measurements of their different parts and a survey of their correlations shows that these are quite numerous. It may suffice to merely point out the parallelism between the average number and weight of the tubers on a plant, the number of stems, and the amount of starch in the potatoes.

Many other instances could be given. They all give proof of a high degree of parallelism between the different organs of a plant, increasing development of one quality being combined with increase or decrease of other points according to definite rules. By this means selection may be guided, as we have seen in a previous chapter. But the cultural treatment may be furthered also by the observation of such correlations, because in stimulating the development of some parts we may expect to increase the size or weight of others at the same time. An exact knowledge of these phenomena is thus of paramount interest for agricultural practice, and the difficult and tedious study of all its features should be diligently carried through until definite principles for the practical work may be derived from it.

Inquiring into the causes of the parallelism of apparently independent characters, we have first to state that it is often difficult to decide whether the observed combinations are due to internal or to external causes. Among the facts I have quoted, there can be no doubt that at least a large majority are due to external influences. On the other hand, more intimate or internal relations may be hidden in some instances without our being able to discern them and thus to classify our group of phenomena. Our only way is to leave them out of consideration until further investigation will have pointed them out and to consider our facts as uniform and as the result of the same causes.

External influences can affect a plant only because of some kind of responsiveness which must be present in it. Without such no reaction will be produced. This assertion may seem to be a truism, but even as such it may help us to reach a better view of the relation under discussion. For it is clear that a parallel action of the external factors demands a corresponding response of the characters to them, and we may base our discussion upon this assumption, making the state of sensibility its chief aim.

As a rule, all variable parts are influenced by the same factors. Among them the nutritive are most prominent. Other agents, such as temperature, moisture, and light, coöperate with these in a more or less considerable degree. Many authors, however, take their significance to be only secondary, inasmuch as the nourishment itself may be changed by them. On the basis of this conception, nutrition would be the main factor in all fluctuating variability.

Now it is evident, that all development depends in the first place upon the amount of available food. This simple sentence gives a key to at least a large group of the phenomena of correlation. Whenever the size of the seeds increases with the weight of the whole harvest, or the number of seeds in a pod with the height and degree of branching of the plant, there can be no doubt that all these qualities depend upon the nourishment, and that it is this factor which causes them all to increase or to decrease at the same time.

This rule will be more easily understood if we take a definite example. As such I choose a variety of cultivated poppies, belonging to the ordinary tall species or opium-poppy (Papaver somniferum). Numerous forms of this beautiful plant are cultivated in our gardens. The most peculiar among them is the variety in which the stamens are partly converted into pistils. These secondary pistils

surround the capsule by a large crown of slender and green organs, which persist after the petals and stamens are fallen off, and thus heighten the ornamental effect of the fruits. Only the innermost rows of stamens are changed in this way. Both the filament and the anther are affected, the former being dilated into a sheath, in whose cavity the ovules are produced. Ordinarily these latter are only imperfectly developed and the bright crown of secondary pistils contribute little if any to the fertility of the flower.

What makes this variety especially suitable for our discussion is the high degree of variability in the development of this crown of pistillodous stamens. In some instances it is seen to be so broad as to have affected a large majority of the stamens; in others only one or two of these parts are changed, and in extreme cases only a single hardened and persisting filament without an ovarial cavity and without stigma indicates the type. All intermediate forms may be found and the variability covers a range, going from one pistil up to a hundred and fifty and sometimes even more. Unfortunately these altered organs often show another anomaly, consisting in a coalescence of some of them, thereby constituting groups, in which it is difficult to distinguish and count the single parts. In extreme cases this coalescence may be such as to combine all the changed stamens into a narrow cup around the normal capsule, and more commonly a more or less divided ring of such groups is observed. It is easily seen that the variability of this character affords an excellent material for the study of its dependency on outer influences. We may make sowings under different circumstances, giving them a sunny or a shaded place, good or bad soil, different qualities of manure, watering or keeping them dry, protecting the young plants under glass or exposing them to all the effects of the weather, and so on. If we do so we easily find that all favorable conditions

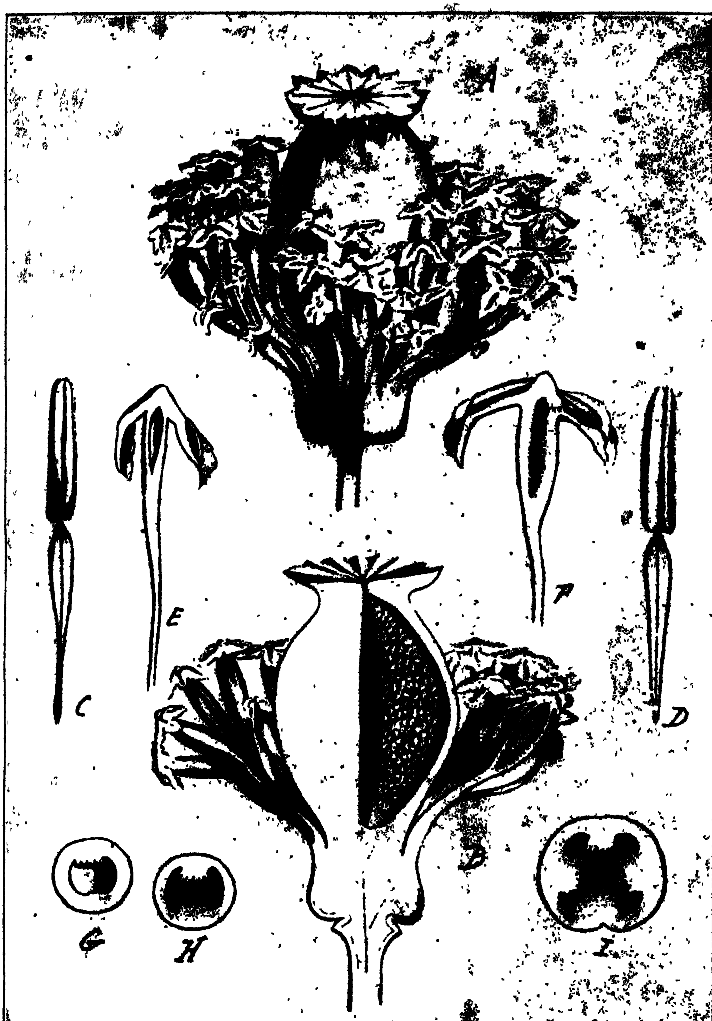

Fig. 92. Polycephalous opium poppy. A. Normal fruit. B. The same cut longitudinally. C, D. Normal stamens. E, F. Stamens transformed into secondary carpels. G, H, I. Secondary carpels, cut transversely with one, two, and four rows of seeds.

increase the crown of pistillodous stamens, while adverse influences reduce the change and thus favor the production of the normal organs.

The same influences, however, govern the degree of development of the whole plant, the height and the thickness of the stem, the size of the flower and the fruit, the number and the strength of the branches, and even the extent of the foliage. Hence we may expect a correlation between the abnormality and the growth of all the normal parts, and it is quite easy to control this. The best means is to choose the ripe capsules. Their size and weight is evidently the result of the activity of the whole plant, during the whole time of its life, and thus may be considered as a standard for comparison.

In a bed of pistillodous poppies, we pick out a group of fullgrown fruits and arrange them according to their size, taking as a measure either the height or the weight of the central capsule without the crown of secondary organs. Then we compare the degree of development of the anomaly with this size, and we find an almost complete parallelism. The smallest fruits are devoid of appendixes or nearly so, and the largest ones bear the richest crowns. Between these extremes the number of the altered stamens regularly increases with the size of the fruit, hardly any deviation from the most complete parallelism occurring.

By this investigation the normal and the abnormal development are proven to be as closely correlated as might be expected. So it is also in other instances. Ordinarily, of course, abnormalities are too rare to permit of such a complete comparison, but notwithstanding this, common experience shows them to be connected with strong growth and favorable life conditions. This relation is often so striking that in former times it was simply assumed that monstrosities could be produced by an excess of nourishment,

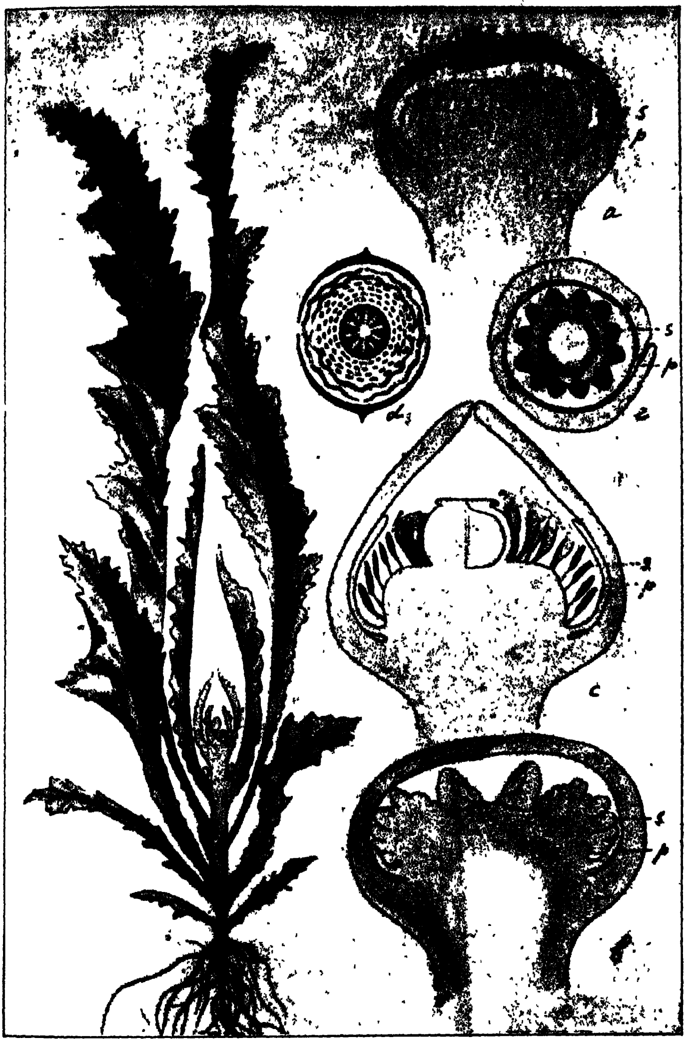

Fig. 93. Young plant of opium poppy in the sensitive period of the development of the terminal flower, cut longitudinally. A. Flower-head of June, 7. B. June, 14. C. All parts discernible. D. Diagram of flower. E. Diagram of young flowerbud. P. Petals. S. Stamens.

but at present it is known that the faculty of producing them must be present beforehand, and that the food-supply can only stimulate the frequency of occurrence and the degree of development.

We may now proceed one step farther and inquire into the time at which the external influences can affect the size and the form of the organs. It is evident that these agencies must be limited to the period of youth, because as soon as the growth ceases, no further change is possible. Here, however, the form and the size must be considered separately, the form being definitely fixed long before the size of the organ is determined. We thus come to this conception in regard to periods of sensibility, that the one for the form ceases earlier than that of the ultimate increase.

The pistillodous opium-poppy may once more be chosen as an example. If we examine a young plant six or seven weeks old we find a short stem bearing a group of leaves which surpass it in size many times. The young bud of the flower is attached at the head of the stem. Its calyx covers the innermost parts, which are still very small. The central capsule hardly begins to be differentiated and the whorl of stamens is seen as a smooth wall of soft tissue around it. At this period the normal and the pistillodous stamens are still awaiting the first manifestation of their form. Shortly afterward they may be seen as small protuberances, rounded and without distinct form, but gradually increasing and assuming more definite types. At this time there is still no visible distinction between the normal and the pistillodous stamens, and it is not possible to decide whether the bud would grow into a rich or into a poor representative of the variety. A few days afterwards, however, the decision becomes apparent, and the period of sensibility closes.

Exact limits for this period of sensibility to the external

Fig. 94. The double corn-marigold, an experimentally produced variety.

life-conditions cannot, of course, be set from these observations. But we do not need them for our present discussion. The main fact is that all organs and qualities must go through such a responsive period, and that this period coincides, at least partly, with their extreme youth. Hence we may derive a general rule for the correlations depending on fluctuating variability. For it is evident that, with the continuous change of the weather, only such organs are really exposed to the same life-conditions, as are sensible to them at the same time. As soon as the period of sensibility has passed, the weather can no longer have an influence, but new parts are produced which will be exposed to the influences prevailing at that time. In this way we may conclude that one of the great factors of correlation is equality of age, because it exposes the organs, during the period of their sensibility, to the same conditions.

Another cause of correlation may be looked for in the mutual dependency of different organs, the one affording or controlling the nourishment for the other. This case, however, though of quite common occurrence, cannot always be easily separated from the first, both causes ordinarily combining their efforts in the same direction.

It may be studied by the statistical method. A hundred or more individuals are measured, and the result is represented by a single line. In order to do this, the individuals are arranged according to the degree of development of the measured quality. Suppose we compare the amount of sugar in the sugar-beets of a field. This amount can be measured for a part of the tissue, without sacrificing the beet, allowing thereby the selection and the ulterior cultivation of the best samples. As is generally known the sap is pressed from the tissue and after clearing it, the percentage of sugar is determined by the method of polarization. In the year 1896, I had an opportunity of studying these percentage

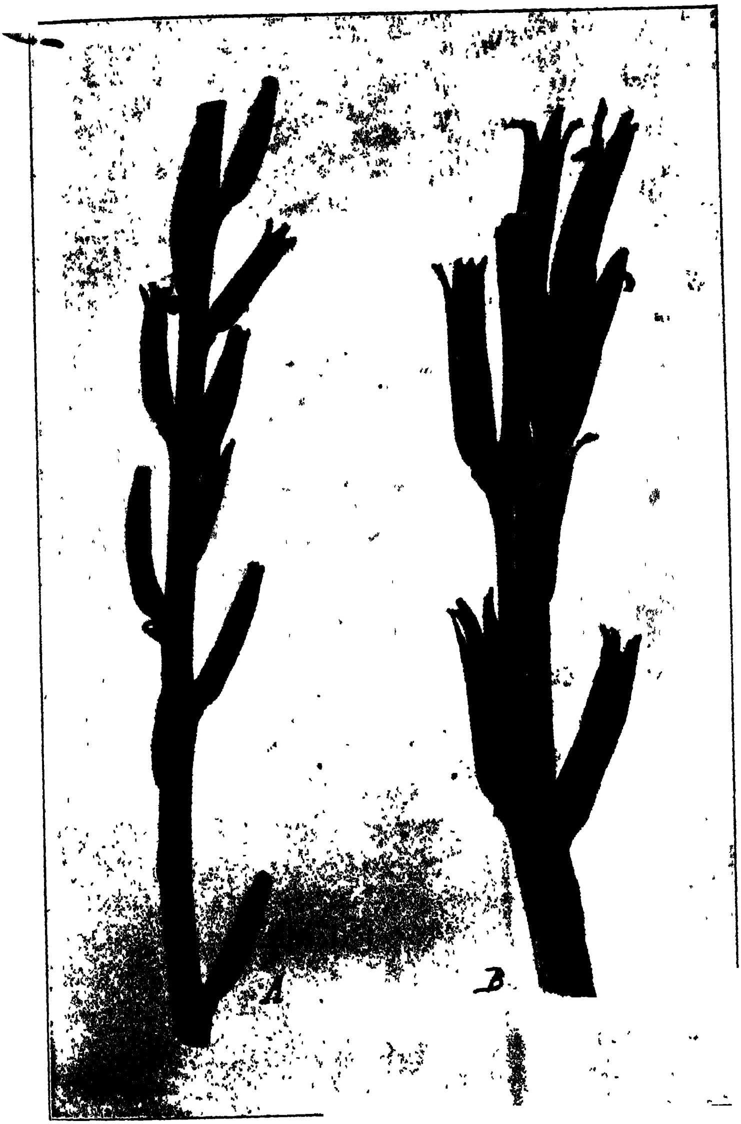

Fig. 95. Variability in the size of the ripe fruits of the Evening Primrose of Lamarck. A. A weak plant with small fruits. B. A tall plant with large fruits.

figures for some 40,000 beets, cultivated on the fields of Messrs. Kuhn & Co., at Naarden, in Holland, and examined in their laboratory for purposes of selection. The average percentage was 15.5, the extremes going up to 19 and coming down to about 12 per cent. These extremes, however, were comparatively very rare, especially on the upper side of the group, where only a few individuals reached the very limit. More than one half of all the beets differed less than one-half per cent from the average, the total number of roots with 15 to 16 percent sugar being about twenty-two thousand. On both sides of this central group the number of beets rapidly decreased with the increasing degree of deviation from the average value.

In the same manner the fluctuating variability of other qualities and other characters may be given under the form of a curve. The ray-florets on the heads of the composites can easily be counted for hundreds and even for thousands of single flower-heads, and the figures thus obtained will show a similar grouping around an average number. In the marigolds this number is 13, in the daisies 21, and the same figures are met with on the flower-heads of numerous other species. The size of fruits and capsules may be treated in the same way. I measured the capsules of over five hundred individuals of an evening primrose and got a curve that did not differ essentially from that of the sugar beets just mentioned. The average individuals bore capsules of nearly 2.5 cm. and the extremes reached 1.5 and 3.4 cm. The largest capsules were thus seen to have about double the size of the smallest ones. Between these limits the different sizes were grouped in such a way that more than half of the individuals could be said to have fruits of medium size, the remaining sizes being respectively rarer the more they differed from the average.

If now we compare this size of the capsules of the evening

primroses with the remaining qualities of the plants, we observe a definite case of correlation. Small capsules are the product of weak stems, long ones are borne only by stout individuals. A curve, made for the height of the plants would run nearly parallel to that of the capsules. Comparing weak branches with the main spike, we find the same arrangements, the capsules on the former being decidedly smaller. I have made some cultures with this species in order to study the correlation of the capsules and the general degree of development under the influence of different outer conditions of life. By giving more manure, a better exposure, or more adequate treatment, it is easy to get much stouter stems, with a richer system of branches and increased foliage. Along with these marks the capsules are seen to increase in size, their medium length coming up from 2.5 to 3.5 cm. and their maximum reaching even 4.5 cm.

It is evident that the growth of the capsules in part runs parallel with that of the other organs of the plant, and in part depends upon them. A stouter stem, with larger and more numerous leaves, produces more nourishment for the flowers and fruits and thereby will make them bigger. On the other hand, the tall individuals are largely those which have found, from their very youth, the most favorable conditions of soil, of water, of exposure, and of other influences, and inasmuch as these factors are still at work during the responsive period of the development of the fruits, they will directly affect them in the same direction. Thus we see that in such cases the causes of correlation are twofold, the one acting directly, the other indirectly, and influencing the younger organs through the degree of development of the older ones.

Returning to the sugar beets, we may give our attention to the correlations which the two main points in their life may exhibit with the more easily appreciated characters

of the roots and of the foliage. One of these two main points, of course, is the percentage of sugar in the sap. The other point is the quality of the seeds, since on this quality the harvest of the next year chiefly depends. Now it is evident that of our two groups of causes which determine the phenomena of correlation of fluctuating variability, only the second one comes into consideration. This correlation may be simply stated by saying that, as a rule, stouter plants will be richer in sugar and produce better seeds. Nearly all other causes, however, which govern the amount of sugar in the roots of the first year will be without influence on the quality of the seeds. Local variations in soil, in moisture, and especially in the amount of space, when this is increased on account of the falling out of some neighbor, will directly influence the sugar percentage, which may also be diminished by insects feeding on the leaves or by other diseases. In the second year the roots will be planted in other fields and with other conditions of soil and exposure, and during the time of production of seeds the single individuals will occupy quite different places on the curve of variability than those they held the first year.

Hence we may conclude that the correlation between the percentage figure for the root of the first year, and the real value of the seeds is only a very feeble relation. The richest roots may yield only poor seeds and conversely. In other words, the percentage figures, which are now the universally accepted criterion for the selection of beets for the production of seed, are only an imperfect indication of the quality of the latter. Direct experiments have often shown the accuracy of this conclusion, and the breeders of sugar-beets know very well that single excellent roots may not be relied upon at all for the production of exceptionally good seed. They rely only on the average of the selected beets, and rightly assume that the larger the group of their roots, the

better is the chance that their seeds will be of superior quality. Selection of seed-bearers based on a direct measurement of their average progeny, as it was originally applied by Vilmorin, seems at the present time to be too troublesome for practice, though theoretically it would be much less open to criticism, and though in the long run it would also yield better practical results.

Such are the laws, which govern that most complicated phenomenon of the correlated dependency of characters and qualities on the outer conditions of life.

E. UNIT-CHARACTERS

The mechanism of an organism consists of numerous parts which are more or less exactly fitted to one another. Nearly all of them are dependent on some others in their development, some profiting by the preponderance of these and others being restricted thereby. Moreover they are governed by the outer conditions of life and these influences change some of them in the same direction and others in an opposite one. Thus we come to the conception of a general interdependency of all parts, organs, and qualities of an organism. They are governed more or less by the same laws which cause them to undergo corresponding changes when subjected to the same influences.

In practice, this interdependency permits the indication of valuable qualities by purely botanical marks, and gives the possibility of basing selection upon marks which may be controlled in thousands of individuals without sacrificing them and without the need of testing all of them directly by their economic value. It is an important principle in plant-breeding, which makes the work more reliable and more available to horticulturists and agriculturists in general. Our great admiration for men of genius may not prevent us from deploring that the improving of our domestic animals and

plants should be laid in their hands only. We wish to know how they work, and how their great achievements are obtained. We wish to study the rules and laws underlying their attainments, in order to apply them to as many instances as possible.

In science, on the other hand, the innumerable cases of observed correlations lead to the question of the more intimate causes of this phenomenon. Our imagination cannot be content with the outward features of the facts; we wish to have some idea of their innermost nature. In this line of thought the principal difficulty lies in the absence of definiteness in the objects we have to deal with. We speak of correlation and interdependency, but we have no idea as to what the things are that should be related to or dependent upon each other.

Here the idea suggests itself that in order to be correlated the characters must begin by being independent entities, which through some later means may come into relation with others. Perhaps this may not be the real way in which nature proceeds, but at all events it is the way in which we should proceed in our analysis. Thus we come to the conception of *units* which govern and control the visible characters and qualities.

A new scope for investigation is opened by this conception. Each organism appears to us as a microcosm, consisting of thousands of elementary entities, which combine to give it its form and functions. The study of these units encroaches upon systematic and comparative sciences, as well as upon the investigations into the physiology and the evolution of all living beings. All comparison culminates in the question as to which units are common to the species under discussion, and which units are the causes of their differences. Systematic affinity is reduced to the same principle. It is founded on the community of a more or

Fig. 96. A. The pansy and some of its parents. B. Viola lutea grandiflora. C. Viola tricolor versicolor. D. Viola tricolor lutescens. After Wittrock.

less large number of units, whilst divergence must evidently be the result of the occurrence of different units. The larger the number of common units, and the smaller that of varying constituents, the greater will be the affinity.

Wide as are the prospects of solving the most difficult problems of systematic science and comparative investigations, and tempting as it is to indulge in a discussion of the possibility of the discovery of their ruling laws on the ground of the principle of units, we must, of course, now limit ourselves to questions more directly concerned with our inquiry.

Among these the chief point is, what is to be considered as a unit? This question is intimately connected with our main subject, and sufficient facts are at hand to draw at least a preliminary sketch. At once it brings us upon the ground of the internal causes of the phenomena of correlation and so completes the scheme made by our distinction between these and the external factors.

Our units may be considered from two different points of view. We may be content with analyzing the visible characters and with reducing them to independent groups, or we may ask for some invisible, although material cause, which constitutes the real source of each unit. This latter inquiry, however, is as yet wholly of a hypothetical nature, and so it may suffice to have suggested it, and to return to the visible features for our further discussion.

There is no reason for assuming that a unit should be limited to one organ, to one tissue, or to one cell. Quite on the contrary, it seems probable that a unit may show its activity in different organs, sometimes even in almost all parts of a plant. This conception affords a broad principle for the explanation of a large group of correlations, the correlated external marks being simply assumed to be the expressions of the same internal character. The faculty of producing a red or blue color may be taken as an instance. If

it is considered as a unit, the tint of the stems and foliage, and that of the corolla and all other parts must no longer be considered as so many separate marks, but as the results of a single intimate character. As soon as this is lost, or reduced to a state of inactivity by the production of a pale variety, it becomes a matter of course that the change at once affects all the colored organs, as we have seen is the case of the thorn-apple, the belladonna, and numerous other instances. The same explanation holds good for the correlation of fissures, as seen in the petals and leaves of celandines and brambles. It is evidently one and the same internal unit which affects both organs.

If this principle of units is true, it must have an overwhelming significance in the study of hybridism. In the first place, all the modes of expression of one unit must steadily keep together, whenever the entire groups of characters are thrown into one another in crossing. This rule must hold good in the more simple cases of crossing varieties of the same species as well as in the hybrids of more widely distant parents. In the first case the rule prevails that the hybrid is not intermediate between its parents, but bears the characters of one of them. Hybrids between blue or red flowered species and their white varieties, between hairy and smooth forms, between spiny and unarmed parents, and many other instances could be presented. They show the marks of the colored, hairy, or spiny parents and are often not at all distinguishable from these. Here the unit is reproduced without being weakened or rather without its divergent expressions being separated from one another. The second generation of the hybrids completely supports this conception. Some plants remain true to the type of the first generation, but others return to the alternative grand-parent. Among red-flowered hybrids whites occur, among a spiny and hairy progeny some smooth ones are seen. But inter-

Fig. 97. Gordon's currant (*Ribes Gordonianum*), a hybrid of the flowering currant and the golden currant.

A B

Fig. 98. A. The flowering currant of the Pacific Coast (*Ribes sanguineum*). B. The yellow currant (*Ribes aureum*).

mediates are still lacking, showing that the unit-character is either present or absent, but cannot be divided into lesser constituents.

Such splittings are even more striking, whenever they are produced on the different branches and flowers of the same individual plant. The instance of the willow-leaved Veronica has been dealt with; its flowers are either of a dark blue or completely white, the unit which produces the dye being wholly absent or present, but not in intermediate degrees. A parallel case is that of the hybrid between the orange and the lemon, which may show the separation of its units within the same fruits, some parts having the color and the juice of the orange and others those of the lemon.

Crosses between species are more difficult to understand. According to the general rule, all the single marks of the parents are mixed up in the offspring so as to form quite a new type. But if we look more closely into special cases, it is often possible to see that definite units of the parents are recognizable in the hybrids, and that their development is often the same, though in other cases checked by the new combination. A notable instance of this rule is a hybrid between the red and the golden currant (Ribes sanguineum and R. aureum), which is commonly cultivated in gardens under the name of Gordon's currant (R. Gordonianum). It has the form and hairiness of the leaves of its red parent, but in the flowers the red and golden colors are combined so as to give an intermediate tinge. The combination, however, is not at all perfect and easily shows on petals and calyx, its two distinct component colors. So it is also in the hybrid of the ordinary and the yellow foxgloves. I have pollinated the first with the dust of the second and had a beautiful lot of hybrids which flowered richly during a series of years. The foliage and spikes were almost those of the yellow parent, the flowers being intermediate in size, yellow, but with a red

Fig. 99. A. The cultivated snapdragon. B.–G. Its color varieties. B. Yellow. C. Delila, tube white and lips red. D–E. Flesh-colored. F. Brilliant, of a fiery red. G. Album, white with a yellow spot on the lip. H. The calyx and the style after the removal of the corolla.

hue, and bearing inside the corolla numerous spots in highly variable numbers. Such spots are seen in both the parents, but most beautifully developed in the red species. Many other instances could be given. The hybrid of the common and the small-flowered evening primroses (Œnothera biennis and Œn. muricata) has the flowers of one and the spikes of the other parent. In the culitivated violets the size and yellow tinge are derived from one of the parents, the Viola lutea grandiflora, and so on.

As a rule some characters of one or the other parent may be more or less easily recognized in the hybrid, but others are so intricately mingled that our knowledge is wholly insufficient to single them out. Each of them may be impeded in its development by the others, and as long as we do not understand the laws by which such mutual hindrances are governed, it is impossible to give more than a superficial analysis.

Crosses may give us an insight into the nature of unit-characters in still another way. Many so-called characters are in reality composite entities and it is by means of crossing that they can be divided into their constituent units. As an instance I select the color of the flowers and especially that of the cultivated snap-dragon (Antirrhinum majus). Its large and bright corollas strike our eyes by their fiery red, and on a closer inspection show a yellow spot on the under lip, and a paler tinge on the tube. These deviations from the general color may be considered as indications of its composite nature. Besides this species a white variety is largely cultivated. It is not absolutely white, but lacks the red dye and the yellow tinge of the main parts. The yellow spot on the under lip, however, has not disappeared, but is still visible, and almost as well developed as in the red species. Here we have the first proof of the building up of the original type out of more simple constit-

Fig. 100. Danebrog opium poppy; petals red with a large white spot at the base.

uents, since the yellow spot is evidently due to a separate unit.

If, now, we cross the red and the white types, we get, according to the ordinary rules, hybrids that bear the marks of the species and not those of the variety. But in the second generation a splitting occurs, and it is this splitting which frees the units from one another. A complete analysis has not as yet been made, but some constituents have been separated and have proven to be real units. Of course, only some of the hybrids have but one unit in a pure condition, others having groups of two or three or even more of them in all imaginable combinations. But the more simple forms are easily recognizable among the throng. In the first place they give proof of the independence of the red and yellow colors. A pure yellow form exists, lacking all of the red. It has two units of color, the one being the spot on the under lip, already mentioned, and the other the general tinge. The red dye is also produced by at least two units, one of them being a fleshy color, equally distributed in all parts of the corolla, except the yellow spot, and the other being of a bright color, but limited to the lips. It is a type called Delila, and distinguished by its colorless tube. As is easily seen, the combination of these two units gives the dark lips and the pale tube of the original species, and this not only theoretically but also experimentally whenever the two constituents are combined by crossing.

In the same way the colors and color-designs of other flowers may be analyzed and their component units separated. The most obvious means for almost all cases is the crossing of the species which has all the units, with the white variety in which they are absent or at least latent. Such crosses usually result in the desired splitting. A most beautiful instance may now be mentioned. It is the separating of the dark central spot of the opium-poppies from the red

of the upper part of the petals. It produces the variety known as the Danish flag and characterized by its broad central white cross on the red field of the petals.

It goes without saying that these splittings may not only be produced by artificial crosses, but must occur also whenever accidental crosses are brought about by insects visiting the variety and the species when cultivated side by side. If this takes place in a nursery, the horticulturist will recognize the new types, isolate them as such, and put them on the market. They will prove constant, or at least become so after some additional splittings. In other words, many intricately colored species must afford, besides their white variety a larger or smaller number of types, in which the constituents of their color-designs are more or less completely isolated. By this means we can study the units by simply cultivating and comparing all the commercial varieties of such a species.

Having thus mentioned the different methods by which unit-characters may become isolated, in order to give proof of their real existence, we now come to the other side of the question. Our conception of units was originally based on the desire of having some principle which might explain the internal causes of correlation, or at least some of them. We have seen that botanical marks observed in the scales of an ear of wheat or barley may be indications of hardiness in winter, of fitness for definite commercial purposes, of resistance to diseases, and other valuable qualities. In order to explain such coincidences, we have assumed that unit-characters are not productive of single marks, but may exhibit their influence in different parts of the plant body. The same unit may become visible in the color of the stem, foliage, flower, and fruit, and so it must also be with other units, which, when added to a type, not only change its flowers or its leaves, but also affect other organs, physiologi-

cal qualities, and perhaps even the whole mode of growth and development.

But if we wish to give a direct proof of this assertion, comparative study is no longer sufficiently reliable. Its units are in reality hypothetical. Their existence may seem to be quite obvious and to be in no need of further proof, but as soon as they are to become the basis for far-reaching conclusions they ought to be beyond all reasonable doubt.

Our question is, when one unit is added to or subtracted from a well-known type, what are the changes which are thereby produced? Now such an addition or subtraction is exactly what we call a mutation, and thus it becomes evident that only directly observed mutations can give a reliable answer. Moreover, mutations are so rare that the chance of two of them occurring together seems too small, or, in other words, that we may confidently assume that each single mutation affects only a single unit.

Considering the mutations of the evening primroses from this point of view, our conception of the correlative nature of the different changes which each of them produces will at once become clearer in its meaning and win the rank of full experimental proof. Some of them are more easily described and understood than others, but the same general rules prevail in nearly every single case.

Let us begin with the short-styled variety or Œnothera brevistylis. Its mutative origin has, as a fact, not been directly observed, but may be deduced from its occurrence on only one native locality and amidst an overwhelming throng of normal primroses. The unity of its character, has, on the other hand, been proven by its behavior in crosses with the parent species. The characteristic mark of this variety lies in the short style which, instead of pushing the stigmas above the anthers, hardly reaches the throat of the tube. Other marks are correlated with this. In the first place,

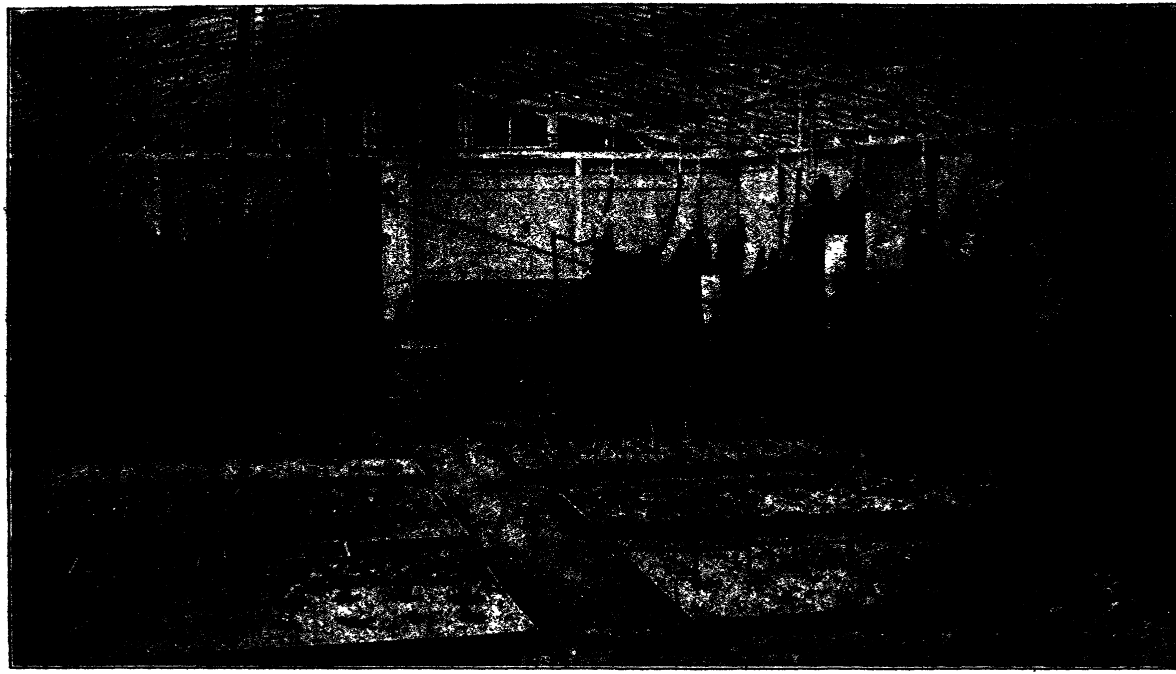

Fig. 101. Glass-covered part of the Experiment Garden at Amsterdam. The biennial plants of the Evening Primroses are flowering; the annual specimens are still very small. Tubes for spraying and sacks for artificial pollination.

some characters of the flower are affected; and in the second place, some of the leaves. In the flowers, the stigma is broadened and flattened and less regularly divided into its four parts. The ovary, which is inferior in the normal species, is here only partially so, and its cavities are seen to protrude above the insertion of the calyx tube, occupying thereby the basal part of the style. How these changes may be brought about by the same cause that shortens the style, we do not understand. But far less can we guess the connection between the marks of the flowers and the foliage. The leaves of the brevistylis have more rounded tips and the plants may, by this means, be recognized weeks before the development of the flower buds, and sometimes even in the rosette stage. This instance of correlation seems analogous to the facts observed among cereals and other cultivated plants. We can only acknowledge the fact from the regularity of the occurrence of the combination, without even being able to guess its cause.

Of course, there are also correlations which we may understand or at least believe we understand. In our case, one of these is seen in the broader flower-buds of the Œ. brevistylis, when compared with the Œ. Lamarckiana. In the latter the calyx is extended by the growth of the style, which presses the stigma from within against its tip. The calyx being thereby elongated, it is only natural that its form becomes more conical as soon as the long style is absent. Perhaps another mark may be explained in a similar way. At the time of the ripening of the seeds the Œ. brevistylis is easily recognized by its very small pods, containing hardly any seed. It may be assumed, although a direct proof is wanting, that the elongation and narrowing of the ovarial cavities within the base of the style is an impediment to the growth of the pollen-tubes, and thus hinders a normal fertilization.

Fig. 102. A. The short-styled Evening-primrose. B–F. Its parent form. *b.* A flower after the removal of part of its petals and stamens. *c.* The same without petals. *d.* The same without the tube and the calyx. *e.* A flowerbud. *f.* Ripe fruits. B–F. The corresponding parts of the parent species. *g.* Styles. *h.* Longitudinal section of ovary. *i.* Transversal section of base of style and calyx-tube.

Exactly similar conclusions may be derived from a discussion of the Œnothera lata, which has often been seen to be produced from the parent species by a single leap. There is even less connection between the various marks by which it is distinguished from Lamarck's primrose. It strikes us through all the periods of its life as quite another type. The very first leaves of the young seedlings differ, being broader and more rounded at the tip. This type of leaves is preserved during the whole life history, and the rosettes, the young stems, and the branches are distinguished by this same mark. There can be no doubt that the form of the leaves during the whole lifetime is regulated by one single unit-character. This unit probably causes still another mark, the extremely sinuous surface of the leaves. Sinuosities, although not lacking in the parent species, are much more numerous in this mutant form. The weakness of the stems and the consequent bending of their tips is more difficult to explain as an effect of the same cause, but it is as constant a mark as the leaves. More curious is the behavior of the flowers. These have only one sex, producing no pollen at all. The anthers are developed and of the normal size, but in their cavities the pollen is sometimes entirely wanting, and sometimes sterile, their place being occupied by the outgrowth of the cells of the inner layer of the wall. These cells commonly collapse and are absorbed, and so it is in Lamarck's primrose and in all its other derivatives, but in the lata they thrive and increase their size until the time of the shriveling of the anthers.

The correlation between the broad and sinuous leaves and this inability to produce pollen is a phenomenon which it is at present far beyond our power to explain. But it is absolutely constant. The lata has been produced anew by the main strain in my garden more than three hundred times. A large number of these plants have flowered, and the flowers

Fig. 103. A biennial specimen of the Evening Primrose of Lamarck.

have always borne the same marks, especially the same deficiency of the pollen. This can be predicted with absolute security from the single inspection of the first leaves of the young seedlings.

Here we have the full duplicate of so many cases of observed correlations, with which we have previously dealt. But in this case the repeated observation of the origin by a single leap may be considered as a direct experimental proof of what, in other cases, can be derived only from comparative studies. In such a case no chance coincidence, no dependency on similar outer conditions of life, and no other hypothesis can adequately explain the facts. Only the assumption that one unit-character may affect different organs of the plant in different and apparently independent ways gives a sufficient idea of their internal connection.

The same correlations may be seen in most of my other mutants. The scintillans and the oblonga are small types, recognizable in their youth by their narrow leaves. The albida is whitish and very delicate and has its peculiar shape of spikes and flowers. The lævifolia combines smooth leaves with a propensity for reducing the petals on the weaker branches to an ovate form. But the most interesting instance and the one which almost exactly corresponds to the correlation between botanical and practically valuable characters of the agricultural crops is that of the Œnothera gigas. Its botanical marks are the dense foliage, the large flowers, the swollen flower-buds, and the small, but thick pods with their less numerous, but bigger seeds. Its cultural feature is its great tendency to be biennial. The parent species and most of its other derivatives can easily be cultivated as annuals, and the rubrinervis evidently prefers this condition. On the other hand, the gigas prefers to develop its stems only in the second year. Under the conditions existing in my experimental garden, it ordinarily defies all endeavors to

Fig. 104. A. Spike with almost ripe fruits of Oenothera gigas, a mutant species. B. The same of Oenothera Lamarckiana, its parent form.

make it flower and produce seeds in its first year. Ordinarily at least one half of the plants remain in the rosette stage, the remainder producing their stems only late in summer or towards the fall, and thus having hardly time enough to display their flowers, and none at all to ripen their fruits.

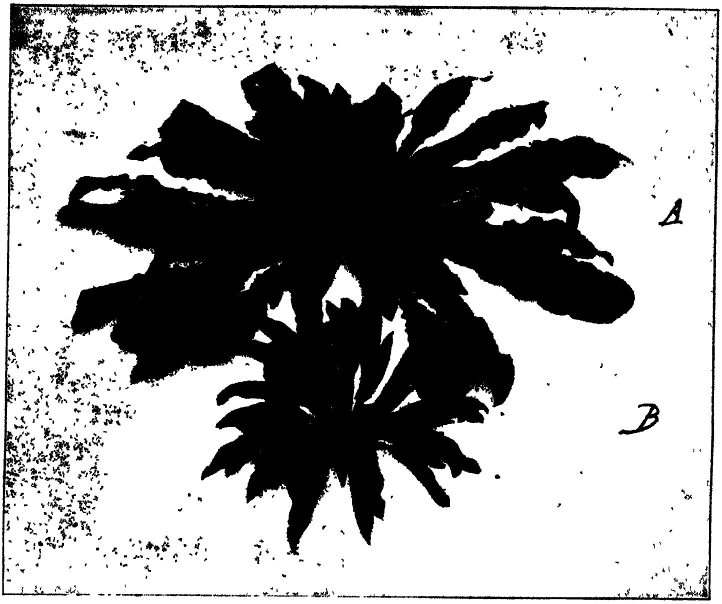

Fig. 105. A. A rosette of rootleaves of Lamarck's Evening Primrose in September. B. A similar rosette of one of its mutants (*Oen. scintillans*) in the same age.

Only in some very favorable years have I succeeded in saving seed from annual gigas plants.

Here we have an instance of correlation such as that between hairiness or form of scales and hardiness in winter or resistance to diseases. But here the mutative origin of the type affords a direct proof of the validity of our assumption that such divergent qualities may be the effects of the same internal unit-characters.

Fig. 106. The smooth-leaved variety of the Evening Primrose (*Oenothera laevifolia*). *a*. A side-flower with ovate instead of obcordate petals, one of the new, highly variable characters of the new form.

By this means the direct observation of mutations supports the conclusions derived from purely comparative investigations. Together they teach us the great law of correlative variability, by which one and the same internal cause may affect different organs and qualities in widely divergent ways. This law intimately connects the scientific results and methods of selection now in use at the Swedish experiment station at Svalöf with the principles and achievements of Burbank in horticultural practice and with numerous other more or less isolated scientific facts and methods of practice. It points out the lines for further investigation. The study of correlations must be carried on on the broadest possible basis. Minute and apparently small marks must be analyzed and compared with valuable properties. Everywhere connections will be discovered. Some of them may be accidental coincidences, and of no further significance, but others will hold good through large numbers of instances. From the broadest possible knowledge of these, new principles of selection will be derived, and slowly, but surely, we shall approach a definite knowledge of the meaning of much that is as yet hidden from our eyes. Then we shall see that there is no mystery connected with the indications which seedlings give concerning the fruits they will bear in later years.

VI

THE GEOGRAPHICAL DISTRIBUTION OF PLANTS

Among all sciences, that of the geographical distribution of animals and plants is necessarily, perhaps, the most international. In crossing the continent of America in order to reach the much beloved far West, my eye was struck by the diversified conditions under which vegetation and agriculture must thrive. Arid deserts and lofty mountains contrast with humid and fertile plains, with large forests and great rivers, with marshes and lakes. Each of these can, of course, be compared with some parts of Europe, and though the impression we get is that of essential difference, the separate parts are as a fact only a repetition of what is seen with us.

The cause of the diversity is, therefore, not to be sought in the climatic conditions, but rather in the special character of the vegetation. In American agriculture corn has taken the place which in Europe is given to the smaller cereals. So it is also in nature. Everywhere the European traveler sees new types and new kinds. As a rule they catch his eye by some common features which are strange to him. Among these, I mention only the rich colors of the flowers in summer and of the foliage of trees and shrubs in the fall.

We are thus impressed with one of the great principles of the geographical distribution of living organisms. We are convinced that the fundamental difference between the organic beings of the two great continents is not, in the main, due to their climates and soils, but that it can have no other cause than their separate origin from the organisms that peopled them in previous geological times. One of the best proofs of the truth of this principle is given by some of the

most common plants of the fields and waste places in California. Immigrants from Europe are of common occurrence, and some plants have spread with a most astonishing rapidity. The Napa-thistle (Centaurea Melitensis) and the wild chamomile (Matricaria Chamomilla) are the most obvious instances, but many other introduced species could be adduced.

It is evident that such new plants are finding conditions here which suit them as well and perhaps better than those under which they live in Europe. The same phenomena are afforded by other species which have been introduced from America into Europe, and are now common weeds or even dreaded pests with us. The Canadian water pest, or Elodea canadensis and the American Azolla (A. caroliniensis) are now perhaps the most widely dispersed obnoxious plants of our canals and ditches, occurring in the largest numbers of individuals.

Such observations are apt to awaken doubts as to the real value of the current ideas concerning the nature of the adaptations of the organisms to their environment. The Napa-thistle and the wild chamomile are evidently as well-fitted for the Californian soil and climate as any of its own native plants. Notwithstanding this, they have acquired the qualities which enable them to multiply in such stupendous numbers here, in another country. Whether in their native localities the soil and the climate were the same, we do not know, but we may confidently assume that their living environment was different, inasmuch as it must have consisted of European plants and animals. And it is generally conceded that living nature has a larger influence on the evolution of new species than the purely physical and chemical conditions.

Our doubt is this: Are the native plants of California still living under the same influences under which they

originated? If this were so, we might assume that their fitness for their present life-conditions has been acquired by means of adaptation. If not, there is no reason at all for explaining their characters on the basis of this principle, and all speculations of this kind are reduced to mere hypotheses, lacking even the possibility of comparative or experimental evidence.

The current conception tacitly assumes that all or nearly all living beings originated on the very spots where they are now found, or, at least, under quite similar conditions. It is evident that only on this assumption the causal connection between environment and characters can help us in explaining the latter. The present life-conditions are called upon to explain the observed instances of fitness in plants.

If, however, plants have as a rule migrated from their native spots, then they are now found in environments which have no right whatever to be considered as the cause of their characters. Quite on the contrary, the migration and the dispersion must have been guided by the nature of the species. Or, in other words: Each plant must have sought out the conditions where it could thrive best on account of its given peculiarities.

Thus we come to the conclusion that the relation between organisms and their present environment is quite the reverse of what it is commonly assumed to be. The properties of the animals and plants must be considered as given facts, and on the basis of these their present distribution is to be explained. It is readily granted that this proposition only withdraws the main point from our study, but on the other hand it brings the investigation along a path of direct inquiry and experience instead of imperfectly founded speculations.

From this point of view the geographical distribution of plants and animals must be discussed under two different

headings. One case embraces the widely-spread species, the other those with a limited area. For the first it is instantly clear that at best only one of their numerous habitats can be the spot where they have originally been produced. To all their other localities they must have been introduced, and, if we do not consider collective forms but pure and elementary types, this must have happened without changing their original characters. Now, the question arises, which locality is their native one? Observation teaches that in almost all instances there is no evidence of a difference between this one and the others. Therefore, it is simply impossible to answer this question in any case with sufficient certainty. It is generally assumed that in the center of the whole dominion of a plant its native station is concealed, but this is only a hypothesis, resting on no observational basis. Quite as well some species might have spread in one direction only, and then their native spot would lie at the very end of their realm. Granting that we cannot recognize this original center of dispersion, we may turn to a discussion of the large majority of the observed localities. Some plants are evidently better fitted for certain stations, while others prefer different life-conditions. The large group of the evening primroses may afford instances. In California only one large-flowered species is met with in the wild state. It is the Œnothera Hookeri which occurs on waste places along roads and railroads, and may even be seen here and there in the parks. It is evidently suited to the climate of California, but its dispersion in Arizona and other neighboring states makes it very probable that it is no real native Californian, but has only been introduced. In this case no single one of its qualities can possibly be explained by the demands of its present environments.

Other species of evening primroses give further proofs. Two of them were introduced into Europe more than a

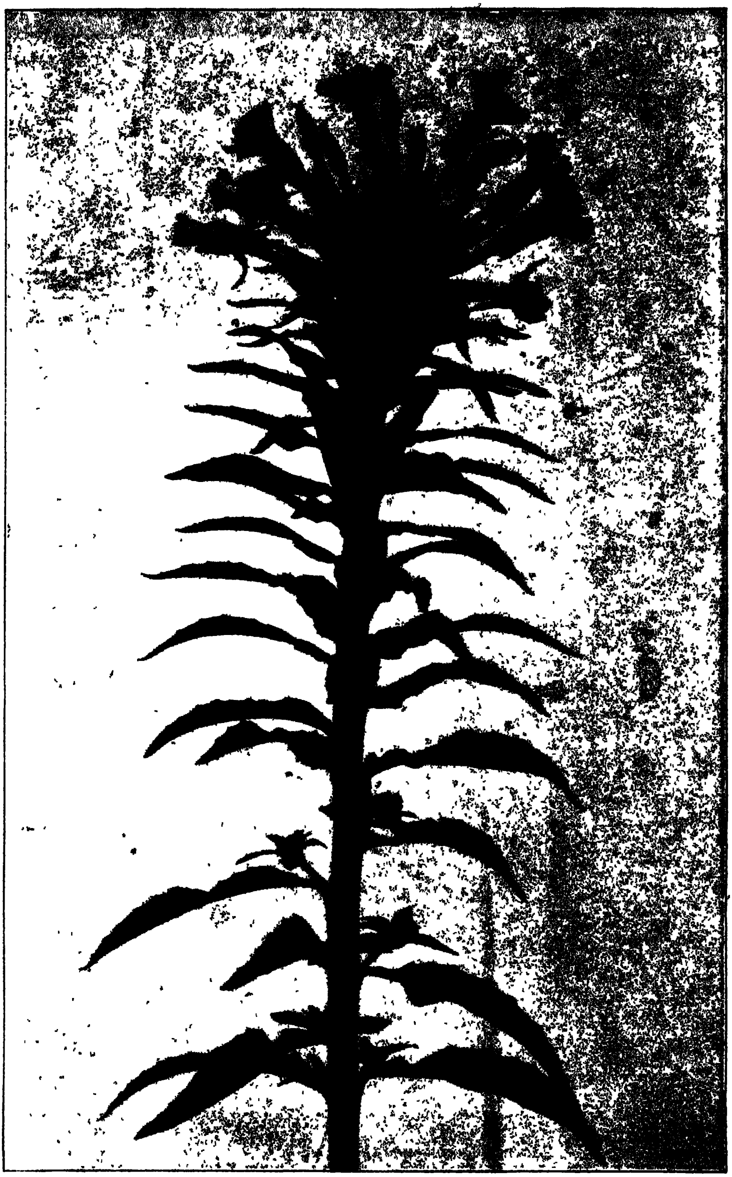

Fig. 107. Oenothera muricata, a seaside plant, which originated far from the sea.

century ago, and have spread widely over various countries. Both have become quite common with us, but prefer different life-conditions. Now it is very interesting to note that one of them, the small-flowered form or Œnothera muricata, prefers the proximity of the sea-shore, whilst the common species or Œ. biennis prefers inland fields and places. On the sand-dunes along the coast of Holland, this difference in stations is very striking, the small flowering type being almost limited to a region of a few miles along the coast.

How can this noticeable difference be explained? Especially, how did the muricata acquire its love for the sea-air and the sea-winds? All our knowledge of the dispersion of the evening primroses points to some part of the middle states of the United States of America as their original habitat, and so it seems evident that even the muricata was originally an inland plant, springing up far from any influence of the sea.

From this special instance we may conclude that at least in many cases, the geographical distribution of wide-spread plants is governed by qualities acquired quite independently of their present life-conditions. Innate propensities govern their dispersion, and have determined where they should be crowded out and where they could multiply themselves. In order to make this conclusion still more convincing, I might draw your attention to the chronological side of the question. We are trying to explain the constitution of forms on the ground of the conditions under which they are now living. But in doing so, we forget how very old they are, and how much nature may have changed since their first origin. Many of our most common species are known to be older than the glacial periods, their fossil remains being found in the upper tertiary deposits (e. g. Statiotes aloides). If they have endured these dreadful

Fig. 108. Wulfenia carinthiaca, which grows almost only on the Gärtnerkugel in Carinthia.

times of cold and of subsequent repeated migration, how can we know under what circumstances they originated? Observation teaches which of the life-conditions available at the present time are the best suited for them, but there is no reason to assume that they have been produced under similar ones. Plants originally inland forms may now prefer the sea-shore, because they are crowded out elsewhere, and many an alpine plant would without doubt prefer a lower and warmer region were it not for dread of the enemies it has to meet there.

Opposed to the common plants, which have evidently migrated far from their place of birth, are the so-called local species, which inhabit only one mountain, or one valley, or are limited even to the slope of a single hill. Here, at first sight, two possibilities occur. The species may be of recent origin, and may not as yet have found time for spreading itself outside of its native spot. Or it may be old, perhaps slowly dying out. In this case it may once have been distributed over large areas, but have disappeared from almost all points. Only there where it enjoyed sufficient isolation or sufficiently suitable life-conditions has it survived. The study of these conditions may then show us the minimum of requirements for continuing its existence, but it does not tell in any way how these precious qualities may have originated. Who does not remember the description of the bright dark-blue Wulfenia, as given by Ouida in her "Moths" (II 271), when Corrèze brought this rare plant from the almost inaccessible heights of the Gärtnerkugel in Carinthia? There it grew upon the slopes of the mountain, and nowhere else in all the world was it found. Evidently it is only a relic of times that have passed away.

How can we determine whether in any given case a local species is nearer its origin than its decline? In most

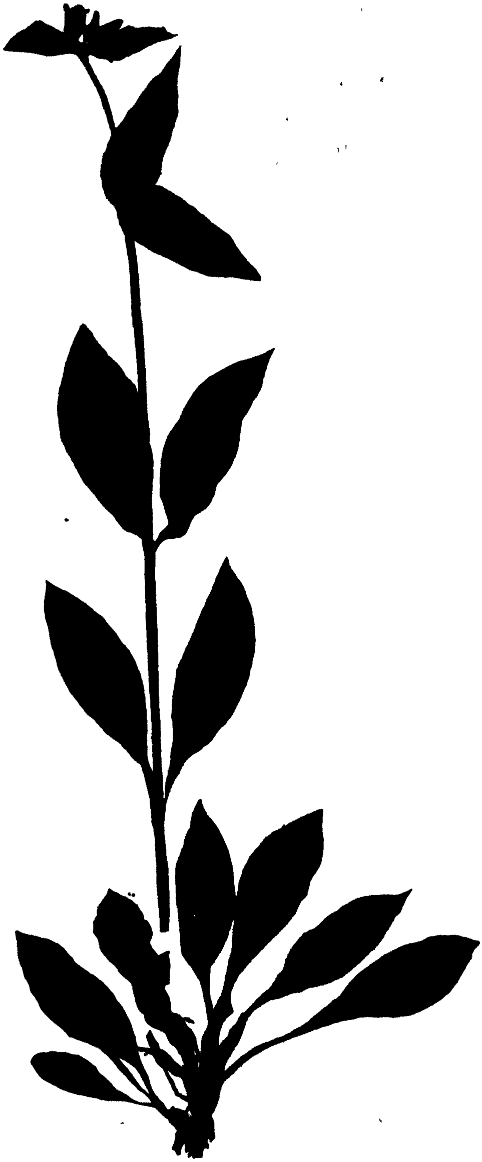

Fig. 109. The smooth-leaved campion, a local plant of Bohemia, with a useless character.

cases, the question is difficult to decide, but there is one instance in which most authors agree in acknowledging the youth of the type. This is the case of the local types of those polymorphic species, whose numerous elementary forms inhabit different stations, but are collected together in the same region. Here the relations between life-conditions and characters may be studied, and the question may be answered on what qualities the occurrence on the observed spots depends. Two instances may be given, since they are illustrative of the real nature of the question. One is a smooth variety of the ordinary campion, which is found almost only in a grove near Münchengrätz in Southern Bohemia (Lychnis Preslii). Here it grows abundantly. But there is no imaginable connection between this mountain-slope or its forest and the lack of hairs on the leaves of the local campion. No other explanation seems possible than that of an accidental mutation, which changed a character in a harmless way and thus left the chances of survival for the new variety simply the same as they were for the species itself. The other case is that of two alpine species of milfoil. They are nearly similar in botanical marks, even to such a degree that their differences may easily be overlooked. They are different, however, in their demands on the chemical constituents of the soil, the one preferring calcareous and the other silicious formations. The Achillea moschata prefers the limy and the A. atrata the siliciferous slopes. In Switzerland wherever both species occur in the same valley they are strictly limited to their particular kind of soil, the one form wholly excluding the other. But as soon as only one species occurs in a valley, it is indifferent to the nature of the soil and grows on lime as well as on silica. Now, how can we tell whether they have originated separately, each on the soil which is now best for it, or whether they had a common origin and have only spread afterward, each

Fig. 110. Two Alpine species of milfoil. A. The Achillea atrata of calcareous soils. B. The A. moschata of siliciferous soils.

multiplying itself most rapidly where the conditions proved to be most suitable?

So it is in many cases. The present life-conditions allow the occurrence of a species whenever they have no relation at all to its special characters, or whenever these characters are fitted for them. If not, a plant may be accidentally introduced and perhaps thrive for some years, but in the long run it will always be exterminated.

The same principle may be applied to the origin of a new form. If its new character is harmless or more or less suited, the type will thrive as well as the parent form from which it derived its origin. If, however, it proves to be injurious, it goes without saying that the form will be condemned to extermination after a longer or shorter struggle for existence. Its only chance of escaping this judgment lies in migration, by which, perhaps, it may find elsewhere more suitable life-conditions.

Returning to our general discussion we may state that the study of the relations of living organisms to their present environment must be revised and rebuilt upon quite new principles. The qualities of the plants are not the problem to be solved. The question is how the given qualities of the species are suited to the environment, and how they enable the organism to hold out against its present enemies, and against the dangers of climate and winter. The question has often been discussed whether we are right in speaking of the use of some character or in saying that a quality serves a distinct purpose. No doubt, much abuse has been made of these terms, and the common assumption that all qualities must serve some special purpose is evidently exaggerated. The only point which is open for inquiry is the question on which marks of an organism depends its possibility of living and multiplying itself on the spot where

we see it, and which other characters are indifferent in the actual struggle for life.

In other words, the principle of adaptation, as one of the main parts of the theory of evolution, should be separated from the study of the geographical distribution. This latter science itself should be divided into two parts, one of which would be concerned with the delimitation of the regions inhabited by organisms of various degrees of affinity, while the second would have to explain the directly observed facts of local occurrence and actual migration. The first of these two parts is a comparative science and is directly related to the theory of the common origin of living beings. The second must become an experimental inquiry into the relationship between the qualities of the plants and those of the environment, which it may prefer or endure. All speculations upon the relationship of organisms to special features of this environment which attempt to explain larger groups of characters on the assumption of some adaptation, are, to my mind, as yet merely poetical descriptions of the way in which we should like to understand and admire nature, but not facts capable of direct proof.

Desert plants afford an instance which may give a clear appreciation of the two contrasting methods of explaining the nature of plants. According to the current view they are most astonishingly specialized and adapted for large regions where it is impossible for other plants to thrive. Although belonging to numerous natural families, and therefore showing hardly any genetic affinity among themselves, they enjoy a group of common features which show the closest imaginable relation to their arid environment. Three main types of desert plants may be distinguished. The most common is composed of the low shrubs with green stems and twigs, a loose mode of branching, and small coriaceous leaves or, in some instances, with no foliage at

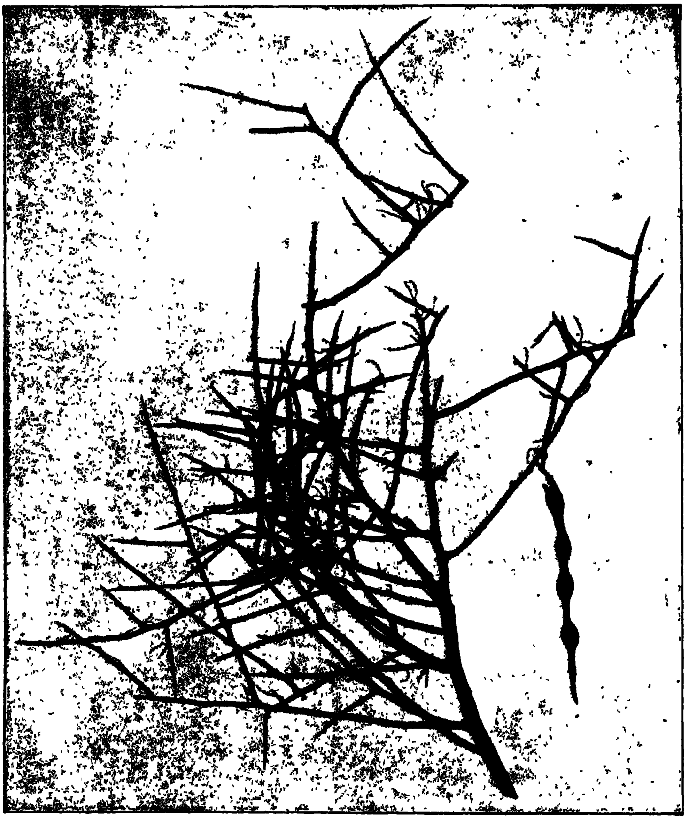

Fig. 111. Palo Verde, or Parkinsonia microphylla, typical desert plant from Tucson, Arizona.

Fig. 112. Palo Christi, or Koeberlinia speciosa, a typical desert plant from Tucson, Arizona.

all. All their visible marks point to a reduction in the use of water, the evaporating surface being as thoroughly reduced as possible. Under the ground, the development of their root-system is quite the reverse. The roots are long and widely branching, penetrating to a considerable depth, thus enabling the plants to procure the necessary water.

The two other types of desert plants are the cacti and the annual weeds. The roots of the cacti are spread laterally, instead of growing to any considerable depth. They may be said to drain the surface all around the plants. They absorb the rainwater at the periods of those short but heavy showers, which for a short time moisten the soil and stimulate vegetation. This water is brought into their fleshy stems and stored up, that it may be used afterward during the long rainless seasons. During rainy weather the stems of the cacti are seen to swell, shrinking again in the succeeding periods of drought. The annual weeds of the desert are distinguished by the shortness of their life-time, this being limited to the few weeks of rainy weather in the spring. As soon as the summer begins and the soil is drying, their life-cycle is completed, and only the dead stems and the numerous seeds remind the visitor of the profusion of flowers which have vanished.

In the mind of a botanist strolling on the arid soils amidst these most strange and astonishing forms of vegetation, the question necessarily arises: Are all these species natives of the desert, and have they acquired their special characters under the influence of the long periods of dryness and the insufficiency of standing water in the soil? Is it the desert which has made them such as they are now, apparently admirably suited for these extreme life-conditions? Or, on the other hand, are they perhaps only a selected few from among the widely differentiated forms, which

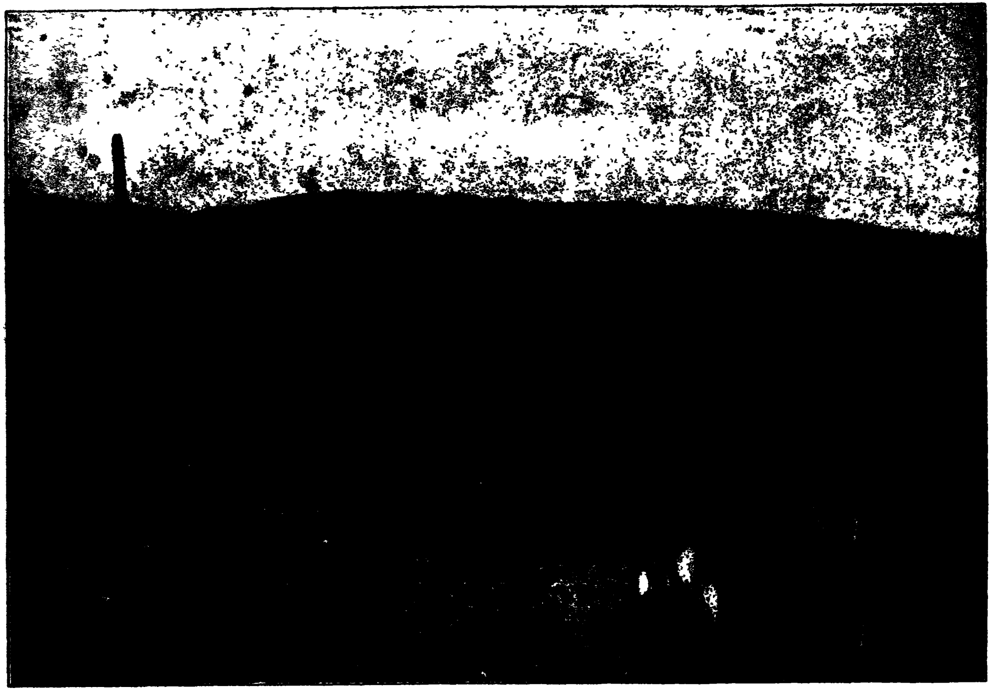

Fig. 113. A forest of giant Cacti (*Cereus giganteus*), near Tucson in Arizona. Opuntia in the foreground. Ocotillo Tree-cactus, and Palo Verde in the middle.

are everywhere abundant in richer regions and on more favorable soils? Are the plants of the deserts only such as can endure the hardships of these unfavorable surroundings, all others being stamped out, as soon as they try to transgress the limits of these peculiar areas? Is not the popular saying that they are cast out, to live on the desert, nearer the truth than the current scientific conception, which regards them as the product of their present environment?

To my mind the answer to these questions is given by the plants themselves. This answer is: They all prefer more favorable conditions to those which are given them. They endure the desert, but only with difficulty. Their life is nearer starvation than enjoyment. They are multiplying themselves in a prodigious manner, not, however, from luxuriance, but on account of the absence of competition. They do not thrive, nor do they unfold their full stature and qualities as they might under better conditions. They greatly prefer irrigated grounds or the moist air of the forest, and only here display their real nature. Even cacti are originally forest plants, and may be seen stoutly growing between densely thronging shrubs. Thus the conviction is forced upon us, that desert-plants are not, as a rule, the product of aridity. They may have originated anywhere else, under any other conditions. But through their peculiar quality of enduring drought, they attained their rapid multiplication as soon as in their migration they reached the arid regions and there found themselves free from competition.

So it seems to me in all those beautiful cases of fitness for peculiar or extreme influences. We do not know how they have been acquired. We may imagine that usefulness in the struggle for life has preserved some qualities, the bearers of injurious characters being easily stamped out. We

Fig. 114. The desert botanical laboratory at Tucson, Ariz., with two shrubs of Ocotillo, (*Fouquieria splendens*), giant cacti, Opuntia, tree-cactus and other shrubs.

may sketch the development of the spurs of the orchids in connection with the length of the proboscis of bees and butterflies, but we cannot directly observe the changes which, we assume, are brought about by such influences. In all those cases it is equally possible, and in some even probable, that they have not been originated in the way in which the plants are now using them. The higher the degree of differentiation, the more probable our mode of explanation may be, but in the more simple and ordinary cases, including the desert plants and many similar instances, the environment has only selected the suitable forms from among the throng, and has no relation whatever to their origin.

Present distribution is the effect of migration, and migration is governed and directed by the given characters of the species. It produces the intimate relationship of the organisms to their environment, to climate and soil as well as to all their vegetable and animal competitors. But in this the qualities of the organisms are the causes, and the distribution is the effect.

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